

HANDBOOK OF THE BIRDS OF THE WORLD

Volume 5

Barn-owls
to
Hummingbirds




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Edited by
Josep del Hoyo
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Jordi Sargatal

HANDBOOK OF THE BIRDS OF THE WORLD



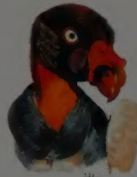
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The *Handbook of the Birds of the World* is, as reviewers never cease to indicate, an astonishing achievement, and their critical rapture has consistently been mixed with a sense of awe – almost disbelief – that such a project should have come to pass. The notion of the time being ripe for so massive an enterprise took many people, myself included, by surprise; but despite the dithering costs of such a project and the dizzying tasks involved in its management, it is certainly the case that much of the basic information on the bird species of the world has now been generated and is available for assembly. A hundred years ago *HBW* would have been unthinkable: so much of the planet remained to be explored, so many species remained to be discovered. Fifty years ago the picture was still very obviously incomplete; and even if new species were by then becoming much harder to find, our general biological knowledge of a high proportion of birds was abidingly feeble. The past quarter-century, however, has witnessed a radical transformation in our information base, as the growth of worldwide tourist markets and the proliferation of Peterson-style fieldguides has elevated birdwatching into a major international pursuit. The rarest birds have accordingly been pursued, their means of surefire identification frequently established, their habits and habitats broadly documented. *HBW* caught the wave and is riding it triumphantly to shore.

From the foreword of this volume, by DR NIGEL J. COLLAR

Jacket illustration by FRANCESC JUTGLAR
Common Barn-owl (*Tyto alba*)
Fringed Coquette (*Lophornis magnificus*)

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Foreword

Risk Indicators and Status Assessment in Birds

*And you know something is happening,
But you don't know what it is...
Do you, Mr Jones?*

– Bob Dylan, *Ballad of a thin man*

Introduction

The *Handbook of the Birds of the World (HBW)* is, as reviewers never cease to indicate, an astonishing achievement, and their critical rapture has consistently been mixed with a sense of awe – almost disbelief – that such a project should have come to pass. The notion of the time being ripe for so massive an enterprise took many people, myself included, by surprise; but despite the dithering costs of such a project and the dizzying tasks involved in its management, it is certainly the case that much of the basic information on the bird species of the world has now been generated and is available for assembly. A hundred years ago *HBW* would have been unthinkable: so much of the planet remained to be explored, so many species remained to be discovered. Fifty years ago the picture was still very obviously incomplete; and even if new species were by then becoming much harder to find, our general biological knowledge of a high proportion of birds was abidingly feeble. The past quarter-century, however, has witnessed a radical transformation in our information base, as the growth of worldwide tourist markets and the proliferation of Peterson-style fieldguides has elevated birdwatching into a major international pursuit. The rarest birds have accordingly been pursued, their means of surefire identification frequently established, their habits and habitats broadly documented. *HBW* caught the wave and is riding it triumphantly to shore.

To shore, to conclusion, to an end; and, when it ends, sometime around 2010 if all goes to plan, there will lie in our hands a truly wonderful resource, a breathtaking work of reference, a masterful avian encyclopedia, a grid of information across the biosphere such as has never previously existed for any major group of animals or plants. And what else? A little less mystery, perhaps; and a lot fewer birds. I do not just mean fewer individual birds, fewer populations, and smaller ranges for almost everything except the human commensals, although this in itself is a deeply depressing prospect; I also mean fewer bird species.

There is, of course, a connexion between these things. It is an odd circumstance – everyone looks forward to the next volume of *HBW*, bearing, as we know it will, the most up-to-date information on a great swathe of the world's avifauna, yet most of us will also have at least an inkling that these new data owe their existence to events over which we may be decidedly less enthusiastic. Birdwatchers and biologists get to ever more remote places – islands, interiors – by virtue of new airports, new logging roads, new tourist facilities. They arrive as tiny components of the great machinery of economic development which, in a few short years, mutilates natural landscapes and human cultures beyond recognition and brings Coca-Cola, television, chainsaws, DDT and debt to every cultivable corner of the planet. By the year 2010 not only will we know more about birds than ever before (and be able to find much of that knowledge in *HBW*); we will also have most of them *completely surrounded*.

We can therefore anticipate learning very early in the new millenium the full meaning of the notion of global stewardship; if not, we will discover instead what it might be like to visit a zoo in which all of the cages are empty. So perhaps the foremost aspiration within this notion must be the absolute minimisation of extinction at the global level. There are, of course, many plans to be devised and implemented in order to staunch the steady outflow of our planet's biological diversity at the distributional, population and genetic levels – all those disappearing individuals – but this is an area riven with political and procedural complexity, and a satisfactory review of the situation, while urgently required, will take several years. Meanwhile we must make no less haste in reaching a better understanding of the early warning signs of endangerment, and a clearer appreciation of the means by which we can confidently and consistently register species as in such danger: the sooner these things are sorted, the surer we can be of preventing too great a taxic haemorrhage by the time *HBW* has run its spectacular course.

A catalogue of risk indicators

We have had many years – indeed, several centuries – to accumulate the evidence; yet we still cannot be confident of all the elements that render species susceptible to extinction. Extinction probabilities appear to vary considerably from one species to another, for reasons we cannot yet – or cannot always – discern; as Simberloff (1986) put it, “Most of the traits said to make a species extinction-prone are eminently reasonable, but... the problem is that for every trait listed one can find species that have the trait and have *not* gone extinct.”

The most obvious and immediate explanation for this problem is that it is traits of one sort or another *in combination* that produce extinctions. Certainly this idea lies behind the widely used metaphor of a vortex to describe the extinction process, where one relatively innocent factor compounds, and is compounded by, other such factors to send a species into an accelerating downward spiral. The interactions of these factors are likely to become increasingly complex as the process of decline continues yet, other than in the skeletal reviews of Frankel and Soulé (1981) and Soulé (1983), I am not aware that an attempt has been made to describe even the simplest of such interactions, although population viability analysis, which models future trends on the basis of different factors at different intensities, seeks to mimic them. It does not even appear that an attempt hitherto has been made, at least as far as birds are concerned, simply to catalogue all the elements that commonly serve in the detection of extinction-proneness.

Meanwhile, since the mid-1990s we have had a widely acclaimed and approved new set of criteria for global status assessment (next section) which champions the use of quantifiable indicators, often in combination. The primary indicators (decline rate, range size and population size) are explicit; however, many secondary indicators (various types of ecological adaptation) are concealed within the general requirement that the criteria will be applied with due consideration of circumstance. The following baseline catalogue attempts to deal with both types, and is offered with three things in mind. First, it may simply be of help in identifying at an early stage the most appropriate species (on the basis of particular geographic areas, habitats, life-history strategies, and so on) for which to be most vigilant. It may also sometimes provide points of reference in cases where quantification otherwise is a matter of informed opinion and decisions to red-list depend on an arbitrary indulgence of the precautionary principle. Finally, it may act as a challenge to fieldworkers to start filling the critical gaps in our knowledge concerning the evolutionary and anthropogenic circumstances of any species suspected to be in difficulties, whether local or global.

In this essay I do not reference information taken directly from Collar and Stuart (1985), Collar *et al.* (1992, 1994), and *HBW* itself.

Distribution

Small range size

For a species to become extinct, its numbers must decline and, in some measurable way, its range size must decrease. Small range size is clearly associated, albeit unpredictably, with extinction risk (see Figure 1). In a small range, any detrimental practices may so rapidly influence the entire population of a species, however abundant it may be (Terborgh 1974), that “extinction is possible within the time span which would be required for conservation measures to take effect” (de la Mare 1987). Perhaps the most notorious example of this was the 1 km² ridge forest at Centinela near Río

Palenque in Ecuador, 10% of whose flora (some 100 species) were estimated to be unique to the site, which was pristine in 1975 and totally cleared by 1988 (Dodson and Gentry 1991). The most notorious avian example may be the Stephen Island Wren *Xenicus lyalli*, whose range was so small that a single cat is credited with its extermination (Rothschild 1907). The need to guard against such catastrophes was precisely what motivated the BirdLife exercise to identify and map "restricted-range" species (ICBP 1992, Stattersfield *et al.* 1998). These are creatures that demand our eternal vigilance, most of which needs to be directed at the distribution and intensity of habitat destruction, and in particular of forest clearance. The threshold of 50,000 km² for a restricted-range bird builds in the opportunity, in many cases, for pre-emptive conservation; conversely, the opportunity for other deleterious factors to make a serious impact escalates with diminishing range size.

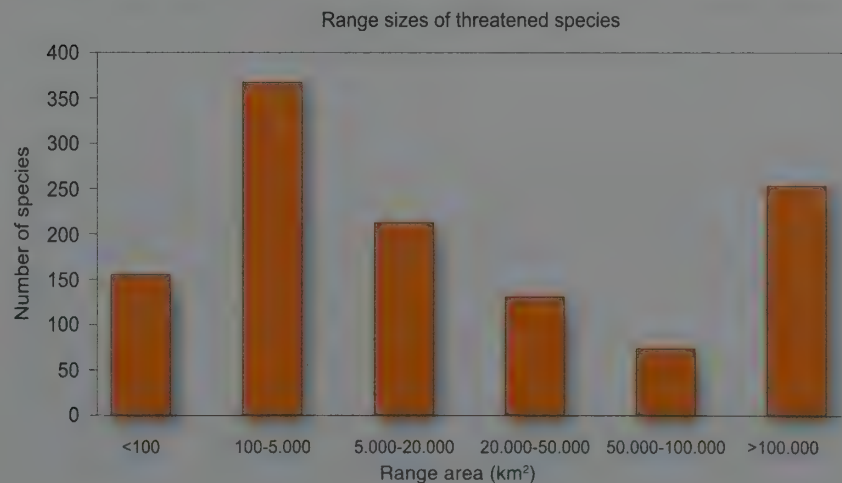
Linear range

Species whose habitats are essentially linear in nature (through confinement to rivers, shorelines, etc.) are exposed to relatively elevated risks from conversion or, more usually, disruption of their habitats, and also because the one-dimensionality of their range greatly constrains total population size. Maps that generalise ranges can give a very misleading idea of the status of such species, which can appear to occupy very large areas and hence to be entirely secure. Recently it was shown that the once-abundant River Lapwing *Vanellus duvaucelii* is highly disadvantaged, in Laos at least, through its confinement to moderately large rivers (>30 m wide), which however are also foci for human settlement and disturbance, and are the persistent target for hydroelectric installations (Duckworth *et al.* 1998). Disturbance, pollution and/or siltation of rivers affect anatids like Blue Duck *Hymenolaimus malacorhynchos* and Brazilian Merganser *Mergus octosetaceus*, sandbank nesters such as Indian Skimmer *Rynchops albicollis* and Piping Plover *Charadrius melodus*, and fish-dependent forest birds like Blakiston's Eagle-owl *Bubo blakistoni*; it can even endanger small birds if they also occupy small ranges, such as the Rufous-throated Dipper *Cinclus schulzi* and Luzon Water-redstart *Rhyacornis bicolor*. Birds of riverine forest like the Wattled Curassow *Crax globulosa* suffer disproportionately if disturbance and destruction of their habitat is compounded by hunting.

Ancient isolates

Islands have been the venue for the majority of recorded avian extinctions since 1600 (King 1985). Confinement to ancient geographical features – oceanic islands, limestone caves, montane and crater lakes – represents a serious liability, owing to the fact that most of the species's evolutionary history has been spent *in situ*, without external contact. Long-term isolation is in itself a defence against the customary "continental" pressures of an evolutionarily diverse environment, so adaptations such as flightlessness and tameness in island birds are traits that have been selected *for* in the absence of predators, but which are dramatically selected *against* as soon as assisted passage allows those predators (but also aggressive competitors and habitat-altering domestic stock) to enter the equation. This type of extinction-proneness has been recognised ever since the demise of the Dodo *Raphus cucullatus*, and the scale of the disaster that convulsed the Pacific in the wake of Polynesian man (Milberg and Tyrberg 1993, Pimm *et al.* 1994, Steadman 1995) has led to the notion that many avifaunas

Figure 1. Range sizes of threatened bird species. Seventy-three per cent of threatened bird species have restricted ranges of under 50,000 km², and c.150 species have tiny ranges of under 100 km² (BirdLife International in prep.).



have already experienced an “extinction filter” (Balmford 1996). Even so, the horrifying loss of the Guam avifauna to the snake *Boiga irregularis* within the last two decades (Savidge 1987) demonstrates that there are still many constitutively defenceless species for which vigilance is needed. These are, however, very difficult cases: no matter how great the precautions, almost certainly something – very possibly disease (Diamond 1984a, Ralph and van Riper 1985) – will eventually slip through the barrier. (It is worth noting that the problem of long isolation extends to Australia, devastated as it is by rabbits, cats and foxes, with birds like the Gouldian Finch *Chloebia gouldiae* and Star Finch *Neochmia ruficauda* suffering from exotic invaders in the form of a parasitic mite and a habitat-smothering vine respectively.)

Political isolates

Confinement to one or two countries is a non-biological circumstance that nevertheless counts as a form of constitutive liability, rendering species vulnerable to the unpredictability of the political or economic environment. Civil unrest in Peru made it extremely difficult throughout the early 1990s to contemplate any intervention – external or internal – on behalf of the Junin Flightless Grebe *Podiceps taczanowskii* (a Critically Endangered ancient isolate). The persistent war within Angola has had the same effect on the rarest Scarp endemics (six listed as Endangered in *Birds to watch* 2). U.S. policy towards Cuba cuts off important potential funding for the conservation of the many threatened birds there, nine of which are unique to the country. No-one can get into northern Iraq to discover the status of bustards, or into southern Myanmar (Burma) to find out if, after over a decade of intense effort for the “last population” in Thailand, Gurney's Pitta *Pitta gurneyi* survives in the Tenasserim tracts. Cambodia, best hope for the Giant Ibis *Pseudibis gigantea*, continues to make virtual bystanders of aid workers and environmentalists. Moreover, when there is serious humanitarian work to do, even the most ardent conservationist is unlikely to feel like knocking on ministry doors; if refugees are camped on the type and only locality of the Somali Long-clawed Lark *Heteromirafr archeri*, then peace be with them. In any case, as everyone knows who has made a long habit of knocking on ministry doors, the influence of corruption in governmental organisations – unenviably underfunded while charged with regulating the exploitation of often enormously valuable resources – is all-pervasive; indeed, the role of political corruption in the erasure of biodiversity is one of those ultimate causes of extinction that cries out for exposure and analysis.

Population

Small population size

Risk of extinction increases with decreasing population size (see Figure 2). Among the forces that conspire to put small populations at increased risk are demographic stochasticity (chance events like an entire generation being the same sex), environmental stochasticity (chance events like storms and fires), genetic deterioration and social dysfunction (Simberloff 1986). The “effective” (roughly meaning breeding) population size is generally used, but many populations possess barely detectable and hence unquantifiable numbers of “floaters”, whose value as rapid substitute breeders cannot be ignored. The debate about what constitutes a minimum viable population size continues to evolve (Franklin and Frankham 1998a,b Lynch and Lande 1998), but it is apparent that some species suffer no great harm from passing through genetic bottlenecks, at least as long as the bottleneck is brief (so that most genetic variation is retained): the Seychelles Warbler *Acrocephalus sechellensis* hit a low of c.50 in 1965 (2,060 in 1997), and the Chatham Islands Robin *Petroica traversi* was down to five in 1980 (250 in 1998) (recent information *per* A. J. Stattersfield).

Population decline

Decline is a clear indicator of adversity (again see Figure 2), and both measuring and explaining decline are crucial to an understanding of the nature and mitigation of the problem. A great challenge for conservation assessment is simply to *detect* significant declines, which can be particularly difficult for species with large ranges, since early status reports (often uncritically repeated, so that they seem relatively recent) can mask modern circumstances. The Spot-billed Pelican *Pelecanus philippensis* and Greater Adjutant *Leptoptilos dubius* once had huge ranges and populations (the former purportedly in millions) focused on Myanmar (Burma), but in the past century these ranges have been “hollowed out”, leaving the pelican moderately secure only in Sri Lanka and the stork at the brink of extinction. Yet neither bird was in the second edition of the international Red Data Book (King 1978-1979); nor – in spite of Stresemann and Grote's (1943) concern, which, alas, found expression in the wrong

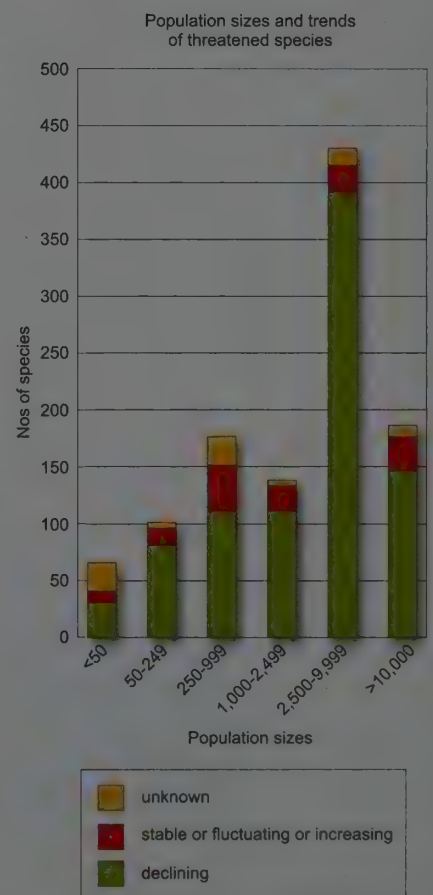


Figure 2. Population sizes and trends of threatened bird species. Seventy-six per cent of threatened bird species have small populations of under 10,000 individuals, and 72% are declining. More than 300 species have tiny populations of under 1,000 (BirdLife International in prep.).

language at the wrong moment (back to political isolates!) – was the now unfindable Slender-billed Curlew *Numenius tenuirostris*. These birds will not have died off – or died back – entirely in vain if only they serve as warnings to maintain the monitoring and red-listing of free-falling species like the Lesser Kestrel *Falco naumanni* and Marbled Teal *Marmaronetta angustirostris* until such time as the declines are understood and tempered. Most of all they serve simply to indicate that the regular gathering of good-quality information on the status of all species is essential to detect declines before they take on terminal characteristics.

Fragmentation

The number and size of subpopulations (difficult to judge though they often are), in particular the size and condition of the largest of them, may have a direct bearing on the fate of species and their need for management. Part of the concern is that highly sedentary species will end up in a series of essentially independent subpopulations, none of which is sufficiently large to avoid long-term effects of inbreeding (some Himalayan galliforms such as Cheer Pheasant *Catreus wallichii* and Blyth's Tragopan *Tragopan blythii* are perhaps strong avian examples). Moreover, modelling of sink/source dynamics shows that, even in more vagile species, the majority of individuals can sometimes reside in non-sustaining subpopulations (Howe *et al.* 1991). Of course the relative productivity of different subpopulations can only be discovered through long-term study of breeding success and survival, but a body of evidence is emerging that elevated predator incursion, diminished food supply and other factors conspire to render many small fragments essentially unproductive (Kattan *et al.* 1994, Turner 1996, Robinson 1998). Certain guilds of bird appear to suffer disproportionately from fragmentation, including large raptors, large canopy frugivores and large terrestrial or near-terrestrial insectivores (Terborgh and Winter 1980, Diamond 1984b).

Ecology

Habitat choice

A species's choice of habitat determines its fate. Habitat destruction is now the most important cause of extinction, responsible for 50% of continental and 20% of island bird losses (Diamond 1984a), and it is much the greatest cause of bird endangerment (Collar *et al.* 1994, 1997). However, habitats are distributed unevenly and differ in the types and levels of human pressure they endure, so the way that measures of habitat are used as indicating susceptibility will vary widely. Simply the rate of decline in some more circumscribed habitats, and simply the extent of others, is evidence enough to red-list some species, on the basis of traits already discussed. The phenomenon of extreme lowland rainforest specialism described by Wells (1985) in Malesia predicates whole suites of species with special needs. Natural patchiness may reflect camouflaged historical or ecological processes (Diamond 1980) and may in turn be camouflaged by generalised range maps, leading (as indicated above) to serious misjudgements of status. Confinement to habitat dominated by single plant species is usually better expressed as a feeding or breeding specialisation (see below), but Kirtland's Warbler *Dendroica kirtlandii*, with its remarkable summer requirement of stands of 8–20-year-old Jack Pines *Pinus banksiana*, is perhaps an exception. Habitats can, of course, be optimal, suboptimal or marginal, and their relative values can only really be identified by long-term studies of breeding success and survival rates. (Perhaps it should also be noted here that over the next century global warming can be expected to shrink many already severely reduced habitats, causing them and their species to wink out in ways over which we are, on present form, unlikely to have the slightest control.)

Indirect upshots of habitat destruction include (a) the breakdown of barriers that keep two species apart, resulting in hybridisation and, in some cases, genetic swamping of one species by the other (Australia's Black-eared Miner *Manorina melanotis* is in this kind of trouble); and (b) the disproportionate benefit it gives to certain brood parasites, resulting in small local populations of hosts suffering total reproductive failure (the Brown-headed Cowbird *Molothrus ater* now jeopardises three species, while the Shiny Cowbird *M. bonariensis* does the same, actually or potentially, for several more).

Habitat sensitivity

Complex stable communities, which generally involve a high proportion of sedentary “equilibrium” species (*K*-selected; see below), tend to simplify under stress. This is one of the great take-home messages of ecology: if a pristine ecosystem is disturbed, for example by hunting or by logging, then *some* components of that ecosystem will

suffer (Erwin 1988, Brown and Brown 1992, Johns 1997, Whitmore 1997). The widespread view that natural resources must provide economic benefits in order to win vital conservation support is often expressed in the compelling, rebarbative phrase "use it or lose it"; but the truth is that to use it *is* to lose it – some of it, anyway. The sensitivity of certain bird species – notably terrestrial and lower arboreal insectivores – to habitat modification (e.g. Lambert 1992, Thiollay 1992, Marsden 1998) needs systematic documentation, and the equilibrium of their environments must be strictly maintained: for example, protected areas within their ranges will have to be managed in such a way that large cores are kept free of human perturbation. The phenomenon of trophic simplification has been shown on land and in water; notably the loss of top predators destabilises communities by allowing the increase of smaller predators, thus causing surges and drops in numbers further down the food chain, and shaking out a number of species altogether (Terborgh and Winter 1980, Lowe-McConnell 1987, Soulé *et al.* 1988).

Seasonality

Migration increases the number of areas, habitats and food resources that a species depends on, and while, in the absence of anthropogenic influences, this predicates no greater inherent vulnerability, the risks certainly multiply when the global environment is patchily deteriorating. Migration therefore also creates a much more complex information requirement, relating to each site and stage of the annual or life cycle. Radio-tracking of Resplendent Quetzals *Pharomachrus mocinno* and other Central American montane bird species has demonstrated their unexpectedly complex patterns of habitat dependence through the year (e.g. Powell and Bjork 1994), and these findings are matched by the discovery of different habitats and strategies used by male, female and juvenile warblers over the non-breeding period (Hutto 1998). Although the problem is clearly most acute for species with already highly circumscribed ranges, even very widespread species can be compromised; I strongly suspect that the loss of the Slender-billed Curlew is attributable to loss of its staging grounds – presumably the Russian steppes – between summer and winter quarters, and equally I guess that the Eskimo Curlew *Numenius borealis* failed to recover its numbers owing to the obliteration of the prairies, which it was known to use on spring stopover. Moreover, where species form seasonal concentrations, as the Eskimo Curlew certainly did, they elevate their susceptibility by temporarily reducing their range size (see above); and where they move to areas inaccessible for political reasons, they jeopardise all the endeavours made elsewhere on their behalf.

Feeding specialisation

Feeding specialisation is a high-risk/high-return strategy. The return is that competition for the resource is minimal; the risk is that disappearance of the resource is terminal. Mistletoe specialists, like White-cheeked Cotingas *Zaratornis stresemanni* and Painted Honeyeaters *Grantiella picta*, and fig specialists, like Large Green-pigeon *Treron capellei* (Lambert 1991; see Figure 3) and Pesquet's Parrot *Psittichas fulgidus* (Mack and Wright 1998), face serious consequences if particular trees or particular tracts are cleared. Too singular a dependence on one species of palm may lie behind the disappearance of the Glaucous Macaw *Anodorhynchus glaucus*, and it certainly lies behind the critical imperilment of Lear's *A. leari*; indeed, any strong dependence on fruit or nectar represents a risk when local climate and habitat loss conspire to isolate these resources in both time and space (a fragmentation issue). The Kaka *Nestor meridionalis* needs insect-derived honeydew to bring it into breeding condition, but introduced wasps also favour this resource and are getting to it first. Rats may have removed the prey-base of the presumed extinct Snail-eating Coua *Coua delalandei*, and medieval man certainly did so with the Canarian Black Oystercatcher *Haematopus meadewaldoi*. A single pair of Siberian Cranes *Grus leucogeranus* needs miles of narrow tundra lakeshore vegetation in which to find the food to rear its single offspring (Potapov 1992); this discovery illuminates the difficulty such a *K*-selected species has in recovering from losses elsewhere in its range.

Nomadism

Nomadism is a distinctive form of food specialisation in which a species is liberated (or driven) from a geographical position for all or part of the annual cycle and then ranges erratically within often very wide limits. Such unpredictability renders conservation planning highly problematic. The Passenger Pigeon *Ectopistes migratorius* was a specialist on a food (mast) that was patchy in both space and time, and which therefore needed social facilitation (strung-out fronts of flying birds) to find suffi-

cient resources to feed and breed: despite the incredible slaughter the species endured, habitat destruction appears to be primarily responsible for its loss, since the patchier the food became, the more difficult it was for individuals to find it (Bucher 1992). Characteristics of nomadic specialisation include (a) high mobility, (b) high investment in social facilitation, (c) some degree of food specialisation, and (d) breeding opportunism. Amongst threatened birds that exhibit some of these traits are the Thick-billed Parrot *Rhynchopsitta pachyrhyncha* (a pine-seed specialist), Golden-plumed Parakeet *Leptosittaca branickii* (perhaps heavily dependent on *Podocarpus* fruits), Purple-winged Ground-dove *Claravis godefrida* and various *Sporophila* (bamboo specialists, as perhaps was Bachman's Warbler *Vermivora bachmani*).

Breeding specialisation

Hole-nesters tend to be forest and woodland climax species, making use of mature, senescent and dead trees large enough and (at least in parts) rotten enough to house them over the breeding cycle. Large-bodied birds like hornbills necessarily require massive trees; but in parts of Australia even moderate-sized species depend on extremely slow-growing eucalypts, some of which are believed to take half a millenium to reach an age at which appropriately deep splits and fissures begin to appear in their upper trunks and branches (Mawson and Long 1994). Studies on the island of Sumba in Indonesia have shown that the hole-nesting avifauna of a forest tract may entirely depend on a small number of particularly large trees, often figs (Marsden 1995). Forestry management regimes which fail to take account of these facts stand to wipe out entire groups of species. Obligate bank-nesters are also constrained: the Blue Swallow *Hirundo atrocaerulea* utilises Aardvark *Orycteropus afer* burrows and pot-holes, while the Three-toed Jacamar *Jacamaralcyon tridactyla* needs stream-hewn banks in forest remnants: both species are uncomfortably constrained by these circumstances. White-necked and Grey-necked Picathartes *Picathartes gymnocephalus* and *P. oreas* need boulders and rockfaces inside primary forest on which to build their nests, which are consequently easily and repeatedly plundered by human nest-despoilers. The Edible-nest Swiftlet *Aerodramus fuciphagus* suffers the same problem, and indeed this, along with other cave-nesting swifts and the Oilbird *Steatornis caripensis*, share with many seabirds and some megapodes, including the threatened Maleo *Macrocephalon maleo*, the inherent susceptibility of being obliged by geology and geography to form site-specific seasonal concentrations (i.e. a temporarily small range size).

Demography

The intrinsic rate of increase (r) in species affects their ability to recover; those with low reproductive rates – called “ K -selected” since they generally occur in highly stable environments whose carrying capacity (K) is permanently at its upper limit – are notably susceptible to depletion by human exploitation, typically driven by maximum profit targets without regard to the long term. Greatly deferred maturity, protracted generation length, high life expectancy and small clutch-size all predict susceptibility. Albatrosses are classic examples, and the loss of only relatively small numbers of some species to the tuna industry's longlines is causing an inexorable population decline, as rates of recruitment fail to keep pace with rates of depletion (Croxall and Gales 1998). Many other seabirds, as well as some of the larger raptors, storks, ibises and cranes, exhibit similar life-history traits that may disadvantage them in the face of direct and indirect human influences.

Economic attributes

Certain kinds of species possess characteristics whose attractiveness to man is clearly disadvantageous. Birds suffer from human over-exploitation for food, for plumes and other body-parts, and for some form of companionship. The key attributes are edibility, visual or vocal beauty, and ease of capture (sometimes also ease of maintenance); cultural and medicinal properties do not seriously figure. Of course edibility is a common condition in birds, but some species are obviously more worth pursuing than others: among the more usual targets are (a) large-bodied, easily snared species of the forest floor, and (b) sociable species such as nest in colonies (especially those tied to specific sites, which simplifies access to their eggs as well), roost in flocks, and come to decoys. For some people, inevitably, the beauty of birds is the price they can charge for them, but at least plume-hunting is now commercially extinct and the extensive hunting of birds for ceremonial adornment is largely confined to parts of the Amazon (macaws and other parrots), the Greater Sundas (hornbills) and New Guinea (birds of paradise, parrots and others); possibly the only taxa seriously endan-

gered by traditional use were in the Pacific – *Vini* lorikeets and certain Hawaiian honeycreepers. However, the cagebird trade remains a major cause of endangerment for some birds, although mainly only when in combination with habitat destruction. Vegetarian species are hugely preferred, for reasons of maintenance; within this subset, parrots are prime targets because of their colours, mimicry and domesticity. Such a combination of attributes is, however, rare in other major groups of species, many of which suffer from intense local rather than international interest (Yellow Cardinal *Gubernatrix cristata* in Argentina, Green Avadavat *Amandava formosa* in India, Straw-headed Bulbul *Pycnonotus zeylanicus* and Java Sparrow *Padda oryzivora* in Indonesia).

A system for status assessment

In the 1990s the International Union for Conservation of Nature and Natural Resources (now known as IUCN–The World Conservation Union) established formal criteria for use in evaluating the probability of a taxon becoming extinct (IUCN Species Survival Commission 1994). In the course of 1993–1994, while the criteria were still being finalised, BirdLife used them to determine the species in *Birds to watch* 2 (Collar *et al.* 1994). Thus the first and second volumes of *HBW* reflected BirdLife/ICBP use of the old IUCN criteria, as applied in the most recent Red Data Books (Collar and Stuart 1985, Collar *et al.* 1992) and the first *Birds to watch* (Collar and Andrew 1988) – this last requiring a degree of interpretation for the Asian and Pacific species since it did not attempt to allocate categories to species. Since 1994 *HBW* has been able to draw on *Birds to watch* 2, and from 2000 there will be a further and much more detailed revision which will serve thereafter as the point of reference for species status in the *HBW* accounts.

The old IUCN criteria for classifying threatened species consisted of five comfortably vague (but, with common sense, perfectly serviceable) status categories, two of which explicitly indicated probability of extinction and three of which did not. These have now been replaced with a much more demanding (but equally serviceable) set of criteria, subcriteria and qualifiers, all of which are related to three categories of threat expressing different probabilities of extinction within particular time-frames. The huge advantage of this new system is that it forces a degree of translucency and consistency into a process which previously offered shelter from these things (and therefore freedom from public accountability, something which ran the risk of bringing discredit to the entire red-listing enterprise).

The new criteria depend on the user being able to make *some* credible estimate of numerical circumstance. As noted earlier, a species can only become extinct by losing its numbers and shrinking some aspect of its range, and these are the two obvious things to measure when seeking to evaluate whether the probability of extinction is increasing for a taxon or not. So the five measurements available are: (1) high rate of population decline irrespective of overall numbers; (2) significant rate of population decline linked to range size; (3) significant rate of decline in range linked to population size; (4) three stand-alone population thresholds and a single stand-alone range threshold; and (5) a population viability analysis which predicts extinction within given time-frames.

The new IUCN criteria

After *Birds to watch* 2 went to press, the IUCN criteria were very slightly altered; and they will almost certainly be altered – adjusted – again in the near future. What follows is a brief account of the criteria as they currently stand, but fuller details can be found in the official booklet (IUCN SSC 1994) or at the following websites:

http://www.iucn.org/themes/ssc/redlist/ssc-rl_c.htm
http://www.wcmc.org.uk:80/species/animals/animal_redlist.html

The categories and criteria below are reproduced almost wholly *verbatim* from IUCN SSC (1994); they are also summarised in Table 1. Several definitions needed to interpret the criteria are appended at the end.

Critically Endangered

A taxon is Critically Endangered (CR) when it is facing an extremely high risk of extinction in the wild in the immediate future, as defined by any of the following criteria (A to E):

- A** population reduction in the form of either of
 - (1) an observed, estimated, inferred or suspected reduction of at least 80% over the last 10 years or 3 generations, whichever is the longer, based on (and specifying) any of: (a) direct observation; (b) an index of abundance appropriate for the taxon; (c) a decline in area of occupancy, extent of occurrence and/or quality of habitat; (d) actual or potential levels of exploitation; (e) the effects of introduced taxa, hybridisation, pathogens, pollutants, competitors or parasites;
 - (2) a reduction of at least 80%, projected or suspected to be met within the next 10 years or 3 generations, whichever is the longer, based on (and specifying) any of (b), (c), (d) or (e) above;
- B** extent of occurrence estimated to be less than 100 km² or area of occupancy estimated to be less than 10 km², and estimates indicating any two of:
 - (1) severely fragmented or known to exist at only a single location;
 - (2) continuing decline, observed, inferred or projected, in any of: (a) extent of occurrence; (b) area of occupancy; (c) area, extent and/or quality of habitat; (d) number of locations or subpopulations; (e) number of mature individuals;
 - (3) extreme fluctuations in any of: (a) extent of occurrence; (b) area of occupancy; (c) number of locations or subpopulations; (d) number of mature individuals;
- C** population estimated to number less than 250 mature individuals and either:
 - (1) an estimated continuing decline of at least 25% within 3 years or 1 generation, whichever is longer or
 - (2) a continuing decline, observed, projected, or inferred, in numbers of mature individuals and population structure in the form of either: (a) severely fragmented (i.e. no subpopulation estimated to contain more than 50 mature individuals); (b) all individuals in a single subpopulation;
- D** population estimated to number less than 50 mature individuals;
- E** quantitative analysis showing the probability of extinction in the wild is at least 50% within 10 years or 3 generations, whichever is the longer.

Endangered

A taxon is Endangered (EN) when it is not Critically Endangered but is facing a very high risk of extinction in the wild in the near future, as defined by any of the following criteria (A to E):

- A** population reduction in the form of either of:
 - (1) an observed, estimated, inferred or suspected reduction of at least 50% over the last 10 years or 3 generations, whichever is the longer, based on (and specifying) any of: (a) direct observation; (b) an index of abundance appropriate for the taxon; (c) a decline in area of occupancy, extent of occurrence and/or quality of habitat; (d) actual or potential levels of exploitation; (e) the effects of introduced taxa, hybridisation, pathogens, pollutants, competitors or parasites;
 - (2) a reduction of at least 50%, projected or suspected to be met within the next 10 years or 3 generations, whichever is the longer, based on (and specifying) any of (b), (c), (d), or (e) above;
- B** extent of occurrence estimated to be less than 5,000 km² or area of occupancy estimated to be less than 500 km², and estimates indicating any two of:
 - (1) severely fragmented or known to exist at no more than 5 locations;
 - (2) continuing decline, inferred, observed or projected, in any of: (a) extent of occurrence; (b) area of occupancy; (c) area, extent and/or quality of habitat; (d) number of locations or subpopulations; (e) number of mature individuals;
 - (3) extreme fluctuations in any of: (a) extent of occurrence; (b) area of occupancy; (c) number of locations or subpopulations; (d) number of mature individuals;
- C** population estimated to number less than 2,500 mature individuals and either:
 - (1) an estimated continuing decline of at least 20% within 5 years or 2 generations, whichever is longer, or

- (2) a continuing decline, observed, projected, or inferred, in numbers of mature individuals and population structure in the form of either: (a) severely fragmented (i.e. no subpopulation estimated to contain more than 250 mature individuals); (b) all individuals in a single subpopulation;

D population estimated to number less than 250 mature individuals;

E quantitative analysis showing the probability of extinction in the wild is at least 20% within 20 years or 5 generations, whichever is the longer.

Vulnerable

A taxon is Vulnerable (VU) when it is not Critically Endangered or Endangered but is facing a high risk of extinction in the wild in the medium-term future, as defined by any of the following criteria (A to E):

A population reduction in the form of either of:

- (1) an observed, estimated, inferred or suspected reduction of at least 20% over the last 10 years or 3 generations, whichever is the longer, based on (and specifying) any of: (a) direct observation; (b) an index of abundance appropriate for the taxon; (c) a decline in area of occupancy, extent of occurrence and/or quality of habitat; (d) actual or potential levels of exploitation; (e) the effects of introduced taxa, hybridisation, pathogens, pollutants, competitors or parasites;
- (2) a reduction of at least 20%, projected or suspected to be met within the next 10 years or 3 generations, whichever is the longer, based on (and specifying) any of (b), (c), (d) or (e) above;

B extent of occurrence estimated to be less than 20,000 km² or area of occupancy estimated to be less than 2,000 km², and estimates indicating any two of:

- (1) severely fragmented or known to exist at no more than 10 locations;
- (2) continuing decline, inferred, observed or projected, in any of: (a) extent of occurrence; (b) area of occupancy; (c) area, extent and/or quality of habitat; (d) number of locations or subpopulations; (e) number of mature individuals;
- (3) extreme fluctuations in any of: (a) extent of occurrence; (b) area of occupancy; (c) number of locations or subpopulations; (d) number of mature individuals;

C population estimated to number less than 10,000 mature individuals and either:

- (1) an estimated continuing decline of at least 10% within 10 years or 3 generations, whichever is longer, or
- (2) a continuing decline, observed, projected, or inferred, in numbers of mature individuals and population structure in the form of either: (a) severely fragmented (i.e. no subpopulation estimated to contain more than 1,000 mature individuals); (b) all individuals in a single subpopulation;

D population very small or restricted in the form of either of:

- (1) population estimated to number less than 1,000 mature individuals;
- (2) population characterised by an acute restriction in its area of occupancy (typically less than 100 km²) or in the number of locations (typically less than 5);

E quantitative analysis showing the probability of extinction in the wild is at least 10% within 100 years.

Lower Risk

A taxon is Lower Risk (LR) when it has been evaluated and does not satisfy the criteria for any of the categories Critically Endangered, Endangered or Vulnerable. Taxa included in the Lower Risk category can be separated into three subcategories:

- (1) *Conservation Dependent* (cd) – taxa which are the focus of a continuing taxon-specific or habitat-specific conservation programme targeted towards the taxon in question, the cessation of which would result in the taxon qualifying for one of the threatened categories above within a period of 5 years;
- (2) *Near Threatened* (nt) – taxa which do not qualify for Conservation Dependent, but which are close to quali-

Type of criteria	Main criteria	Sub-criteria	Qualifiers	Codes	
A. RAPID POPULATION DECLINE	Decline >80% in 10 years or 3 generations (CR) involving either 1 or 2:	1. Decline which has happened (observed, estimated, inferred or suspected) based on a-e opposite:	a. Direct observation	A1a	
			b. Index of abundance	A1b	
			c. Decline in extent of occurrence, area of occupancy, and/or quality of habitat	A1c	
			d. Actual or potential levels of exploitation	A1d	
	Decline >50% in 10 years or 3 generations (EN) involving either 1 or 2:		e. Effects of introduced taxa, hybridisation, pathogens, pollutants, competitors or parasites	A1e	
	Decline >20% in 10 years or 3 generations (VU) involving either 1 or 2:	2. Decline likely in near future (projected or suspected) based on b-e opposite:	b. As b above	A2b	
			c. As c above	A2c	
			d. As d above	A2d	
		e. As e above	A2e		
B. SMALL RANGE fragmented, declining or fluctuating	Extent of occurrence estimated <100 km² (CR) with any two of 1,2 or 3:	1. Severe fragmentation or	None	B1	
	Extent of occurrence estimated <5,000 km² (EN) with any two of 1, 2 or 3:				At 1 location (CR)
	Extent of occurrence estimated <20,000 km² (VU) with any two of 1, 2 or 3:				At <5 locations (EN)
	or	2. Continuing decline (observed, inferred or projected) in any of a-e opposite:	At <10 locations (VU)		
			a. Extent of occurrence	B2a	
			b. Area of occupancy	B2b	
			c. Area, extent and/or quality of habitat	B2c	
			d. Number of locations or subpopulations	B2d	
	Area of occupancy estimated <10 km² (CR) with any two of 1, 2 or 3:	3. Extreme fluctuations in any of a-d opposite:	e. Number of mature individuals	B2e	
	Area of occupancy estimated <500 km² (EN) with any two of 1, 2 or 3:		a. Extent of occurrence	B3a	
	Area of occupancy estimated <2,000 km² (VU) with any two of 1, 2 or 3:		b. Area of occupancy	B3b	
			c. Number of locations or subpopulations	B3c	
		d. Number of mature individuals	B3d		
	C. SMALL POPULATION & DECLINING	Population <250 mature individuals (CR) and either 1 or 2	1. Decline >25% in 3 years or 1 generation (CR) Decline >20% in 5 years or 2 generations (EN) Decline >10% in 10 years or 3 generations (VU)	None	C1
Population <2,500 mature individuals (EN) and either 1 or 2		2. Continuing decline in numbers of mature individuals and population structure (observed, projected or inferred) in form of either a or b opposite:	a. Severe fragmentation: all sub-pops<50 (CR) Severe fragmentation: all sub-pops <250 (EN) Severe fragmentation: all sub-pops <1,000 (VU)	C2a	
			b. All individuals in a single sub-pop	C2b	
Population <10,000 mature individuals (VU) and either 1 or 2					
D1. VERY SMALL POPULATION	Population <50 mature individuals (CR)	None	None	D1	
	Population <250 mature individuals (EN)				
	Population <1,000 mature individuals (VU)				
D2. VERY SMALL RANGE	Area of occupancy <100 km² or <5 locations (VU only)	None	None	D2	
E. POPULATION VIABILITY ANALYSIS	Probability of extinction in the wild is >50% in 10 years or 3 generations (CR)	None	None	E	
	Probability of extinction in the wild is >20% in 20 years or 5 generations (EN)				
	Probability of extinction in the wild is 10% in 100 years (VU)				

fy for Vulnerable; (3) *Least Concern* (lc) – taxa which do not qualify for Conservation Dependent or Near Threatened.

Data Deficient

A taxon is Data Deficient (DD) when there is inadequate information to make a direct, or indirect, assessment of its risk of extinction based on its distribution and/or population status. A taxon in this category may be well studied, and its biology well known, but appropriate data on abundance and/or distribution are lacking. Data Deficient is therefore not a category of threat or Lower Risk. Listing of taxa in this category indicates that more information is required, and acknowledges the possibility that future research will show that threatened classification is appropriate.

Not Evaluated

A taxon is Not Evaluated (NE) when it has not yet been assessed against the criteria.

Further definitions

The following terms require definition in relation to the above: *population*, the total number of individuals of the taxon (expressed as mature individuals only); *subpopulation*, geographically or otherwise distinct groups in the population between which there is little genetic exchange; *generation*, the average age of parents in the population; *extent of occurrence*, the area contained within the shortest continuous imaginary boundary which can be drawn to encompass all the known, inferred or projected sites of present occurrence of a taxon; *area of occupancy*, the area within its extent of occurrence which is occupied by a taxon (usually only measurable in terms of the area of its habitat); *location*, a geographically or ecologically distinct area in which a single event will soon affect all individuals of the taxon present.

The problems of data quality and consistency of judgement

The new IUCN criteria are analogous to a piece of legislation: no matter how clear, objective and straightforward they are intended to be, the options and qualifications they possess, in their attempt to cater for different biological and heuristic circumstances, mean that their *consistent* application using anything less than high-quality data is unattainable. Minor loopholes and grey areas allow scope for various interpretations and hence result in variable assessments (Stattersfield 1997).

The fundamental problem is that, despite the ornithological knowledge base being so much broader than it was 25 years ago (enough to write a *Handbook* entry on every bird), it is still insufficient to sustain confident judgements on the conservation status of a significant minority of tropical species. It is not just that there are very few species for which the exact number of individual specimens alive is known, or the exact range. It is also, far more problematically, that assessments of the severity of threats to species, most obvious among them being rates of habitat loss, are commonly (a) out of date, (b) difficult to interpret, (c) incomplete, (d) unquantified, (e) patently unreliable – and any of the foregoing in combination – or otherwise (f) non-existent. Writing this at the start of 1999, I still have no clear idea of what happened in Borneo in the recent notorious fires of 1997–1998, yet the inclusion or exclusion of several Bornean endemic bird species from *Threatened birds of Asia* hangs on *some* understanding of the resultant status of the island's once-extensive forests.

Aside from the birds, which are all reviewed by staff at BirdLife International working with bird specialist groups, species status assessments are generally undertaken by individual specialists on particular groups of animals and plants; but these people are not, and cannot be expected to be, specialists on the status of their species' habitats. It is inevitable that different evaluators will use different background information (not only on threats but also on conservation measures) owing to differences (a) in the accessibility of resource material, (b) in the diligence with which they seek it, and (c) in the interpretation they place on it. For example, in a circumstance where four primary-forest species have the same range, the granting of a logging concession within that range might produce the following responses among four different evaluators:

- A assumes that the concession spells disaster, and classifies CR;
- B believes that it will take a decade to implement, and classifies EN;
- C knows that it is on such difficult terrain that extraction will be modest, and classifies VU; while
- D misses the story altogether, and classifies LR.

In a similar way, differences in panic and information levels over the recent fires in Borneo will doubtless cause equivalent disparities amongst the multiplicity of specialists assessing the conservation status of the island's endemics.

Background (i.e. non-specialist) information can thus be crucial to the red-listing of a species. Moreover, an even treatment of *all* taxa – i.e. *between* evaluators – is essential if there is then to be an equitable distribution of resources to support those taxa as a consequence of their red-listing: it is clearly unsatisfactory that misclassifications based on negligent research can qualify undeserving taxa for – and disqualify deserving taxa from – conservation support. No less importantly, therefore – and this is one of the main reasons for and advantages of Red Data Books as against Red Lists – the background information used in an evaluation needs to be stated, otherwise the entire process remains opaque. This is not just a matter of honesty, for if all that is published is the notation (e.g. VU C2b, a single declining population of under 10,000), then it can easily be assumed by later workers that the population figure is based on hard fact when all it represents is a highly precautionary inference using very slight evidence (Stattersfield 1997).

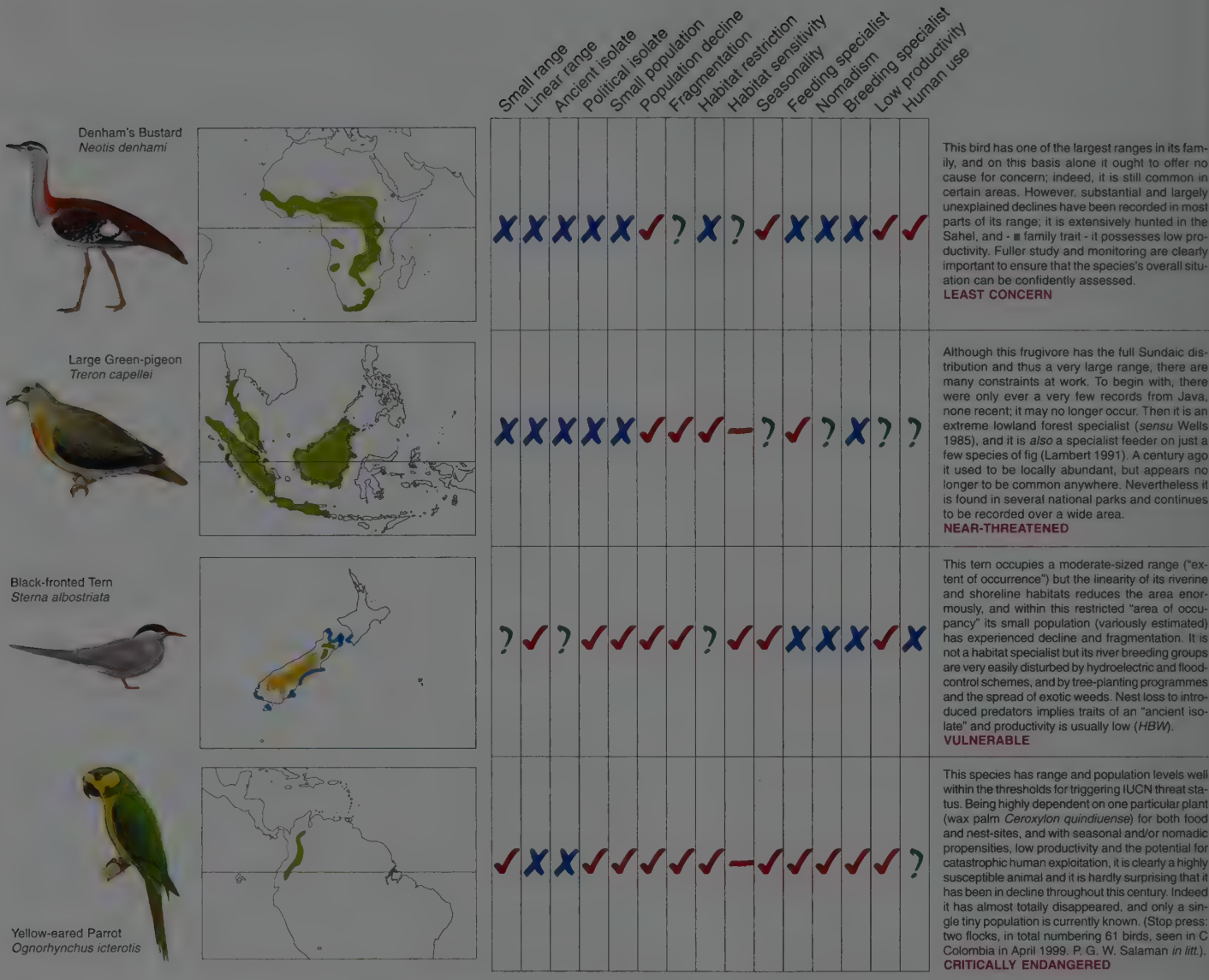
The preamble to the new IUCN system encourages evaluators who find themselves in a data vacuum to “make intelligent inferences” about the taxon they are assessing, and to “apply the precautionary principle” in a credible manner. In practice, of course, the degree of variation in actual or notional estimates relating to the criteria can be so great that what is “intelligent” or “credible” is impossible to decide. The *Birds to watch 2* team coined the term “responsible pessimism” in an attempt to deny the use of the worst-case scenario in making a decision, and to reduce default use of the category “Data Deficient”. Even so, there is always the haunting fear that to go for any more comforting scenario is to risk both complacency and opprobrium, and I strongly suspect that this is a common experience among evaluators, who would far rather be ridiculed for listing a safe species than be vilified for omitting a struggling one.

Perhaps the most problematic aspect of the classification process lies in the significance to be attached to human intervention in its various forms. The category of “Conservation Dependent” was introduced because the degree of active protection a species enjoys cannot be ignored as a determinant of its status, yet the actions taken may not be adequate or appropriate, and even if they are they may not remain so. Governments cut funding to programmes; protected areas are degazetted or simply overrun; projects mistake the causes of the problem they are tackling. In addition, there is real difficulty in assessing the overall relevance and impact of intervention when it affects only relatively small parts of the total range or population of the species; and, for example, over whether species whose ranges are wholly encompassed by protected areas, and which face no threat within them, merit listing at all. These are persistent difficulties which can only be resolved on a case-by-case basis, yet for which consistency of judgement between cases is vital.

Prospects

All risk indicators help identify threatened species, but those that are quantifiable are in a sense more relevant: these are the primary indicators that have been accessed as criteria in the new IUCN system. The ecological attributes are secondary indicators which, by not being measurable in space (ranges) or by numbers (populations), remain essentially more speculative and anecdotal. Nevertheless they have a distinct value in pointing to the kind of species to be considered for red-listing, and in justifying a final decision on categorisation in the absence of more formal numerical data (see Figure 3).

Growth in the composition of Red Lists provides some evidence for the way in which the world is coming to an end – perhaps not a literal end, but the end of an era to be sure. The year 2000 is a ridgetop from which the planet's lovers of wild places can look back at a rich landscape haunted by wasted opportunities, and peer forward at a dustbowl signposted with wasted words, “biodiversity” prime among them. But there can be no turning back, and indeed the next few decades – which means, pretty much, the rest of our lives – will be decisive for the wildlife of the planet for the next few millennia. So if we want the decidedly crumbly future to be worth the walk, we have to set about the pursuit of information and, in direct consequence, the pursuit of conservation, with an altogether new and messianic intensity. There is no reason why this needs to be left to professionals; amateurs can (and do) make a huge difference. The latitude necessarily given over to guesswork and assumption in IUCN status assessments is far too great, but even for the species that are *not* red-listed there are gaping holes in our knowledge which we cannot afford to leave unaddressed for much longer.



Naturally enough it is the threatened species on which we need to focus the maximum effort in generating new data and in implementing sound measures. The BirdLife Red Data Books have been written for people seeking to help with these species, and over the years many fieldworkers, amateur and professional, have taken up individual cases and groups of cases at given sites. For all the other species there is no better single guide to the general state of our knowledge than the *Handbook of Birds of the World*. Many of the primary indicators are discernible in the status sections provided and from the maps, and often the secondary indicators – feeding and breeding specialisations, seasonality, nomadism, demography and exploitation levels – are also accounted for in such a way as to be helpful to the evaluator. So in spite of my disquiet at the means by which our knowledge will be obtained, of course I welcome each new volume of *HBW*, and I look forward to the time when it becomes the hard-copy database for all the world's birds. If that database duly grows broader as a consequence of the individual efforts of *HBW*'s purchasers and readers, then we shall have still more reason to be grateful.

However, the single most important perception that follows from the criteria and, in particular, the catalogue is that the majority of extinction-prone species can only be secured by protected areas, many of them large, many of them strict; only, in other words, by setting aside significant tracts of the planet with the full intention that the factors rendering their inhabitants extinction-prone shall be absolutely minimised. It is futile to pretend that this can always happen, of course, and in already "over-developed" regions like western Europe there are inevitable compromises to be made over multiple uses of the landscape. Equally, however, it is futile to pretend that man and

Figure 3. Four examples of threat assessment and the value of supplementary consideration of risk indicators.

✓ = Yes X = No
? = Maybe - = Unknown

biodiversity are more than modestly compatible bedfellows, for the fate of the great majority of species is directly related to the levels of disruption and destruction inherent in modern human economic activity. Biodiversity is like the Lascaux cave art: the more contact we have with it, the quicker it dissolves away (use it: lose it). So if conservationists, planners, development agents and politicians – the people who most often invoke the term “biodiversity” – *really* want to honour its meaning, then they must understand that their primary responsibility is to defend key areas – and, I repeat, *large* areas – of land and sea from the gross intrusions of the species to which they belong.

Not, of course, that even this will be enough. For protected areas to survive for more than a generation or two, a genuine revolution is needed in human socio-economic activity and relations, involving among other things the integration of conservation interests and practices across even the least natural, most brutalised landscapes. It is an awesome prospect, but one we cannot shrink from: if the green agenda seems never-ending, this is only because we want life on earth to be that way, too.

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Introduction to Volume 5

As ever, readers are referred to the general introduction to the whole HBW series, which appeared in Volume 1 (pages 15-33), while further points of possible interest may be found in the brief introductions to Volumes 2-4.

The trend set in preceding volumes, with each time more plates, more figures illustrated, and more photos published per volume has continued. We trust that this trend meets with our readers' approval, even if it provokes the alarm of the publisher! The two larger families in this volume are backed by over 100 photos each, thus permitting ample coverage of a good range of species. Another new record within the series is that for the length of a single species account: few will dispute that the much-studied cosmopolitan Common Barn-owl (*Tyto alba*) is as good a candidate as any for this award.

As anticipated in the previous volume (see Volume 4, page 26), and in response to readers' letters, it has been decided that the details on restricted-range species and their presence in Endemic Bird Areas are well worth including for the species in question. As defined by BirdLife International, a "restricted-range species" is one which in historical times has had an overall range of under 50,000 km². An Endemic Bird Area (EBA) is an area within which the nearby or overlapping ranges of two or more restricted-range species are wholly encompassed. Restricted-range species account for some 27% of the world's avifauna, or about 2600 species, and these are restricted to about 220 EBA's, which in turn support roughly 75% of all globally threatened bird species. These are thus areas of high priority for conservation, all the more so as they tend equally to be centres of endemism for other life forms.

In recent years BirdLife's data-base has been expanding rapidly towards a situation in which it is possible to give an ever more accurate status assessment for every single one of the world's bird species, as laid out in the Foreword to this volume. It is hoped that from Volume 6 onwards it will be possible to apply these new, more precise categories for all species.

One of the difficulties in producing a global handbook is that within the same language meanings and usage vary in different parts of the world. For example, in some parts of the world height above sea-level on land is commonly referred to as "elevation", whereas "altitude" is considered to refer to height above the ground in mid-air. In contrast, in other regions, "altitude" is used for both concepts; or both words are used indifferently for both concepts; or the meanings given above may, if anything, even be reversed. For the purposes of HBW the two words are used indifferently.

In the same vein, in some parts of the world the hyphenation of bird group-names involves capitalizing the initial letter of the second word in some, but not all, cases (e.g. Barred Owllet-Nightjar). In other regions, or amongst other ornithologists within the same region, it is common practice for the hyphen to be followed invariably by a

small-case letter (Barred Owlet-nightjar). Further versions of the same that are commonly used in different parts of the world involve omitting to use hyphens at all, either keeping the two words separate (Barred Owlet Nightjar) or uniting them (Barred Owletnightjar). Each of these systems has its defenders and detractors, its advantages and disadvantages, but in our opinion none of them is intrinsically "correct" or "incorrect". Within any one publication, however, it is clearly highly desirable to stick consistently to one of the available options. For the purposes of HBW, it was decided to follow the second of the abovementioned methods, in part because this is the system used by BirdLife International, amongst others; for a summary of some of the arguments in favour of this system, see Andrew (1992) *The Birds of Indonesia: a checklist (Peters' sequence)*.

While on this subject, it may be worth underlining that, despite the many major advances in the field of taxonomic study in recent decades, there are few real certainties. Taxonomy is a science of approximation, in which personal subjective opinions are permanently at work. For this reason, relatively few questions can ever be considered definitively settled, as different students commonly apply different criteria.

A couple of notes are necessary regarding the plates. First, in those plates to which it is applicable, the printed scale refers to the "normal" full figures, not to the reduced-scale flying birds, as, for example, in *Stéatornithidae* and *Caprimulgidae*. Second, following standard practice in bird books, the hummingbirds have been painted with most of their iridescent colouring fully visible. In life, because visibility of the colours depends on the angle of incidence, it is essentially impossible for all the colours to be seen by an observer at any one instant, but for the purposes of producing informative plates, this "standard" degree of artistic licence has been repeated for the present volume.

As before, the accepted French, German and Spanish names come from the sources indicated in Volumes 1 and 2. Missing names were again supplied by the relevant committees. Normand David very kindly took over correspondence regarding French names after the sad death of his predecessor, Henri Ouellet. Peter Barthel has continued cheerfully to deal with our problems regarding German names. The list of recommended Spanish names continues to be published periodically, the last batch appearing in *Ardeola* 45(1): 87-95.

Acknowledgements

As each volume goes by, the assistance we have to seek at museums appears to increase! Amongst our most important ports of call have again been the British Museum of Natural History at Tring (Robert Prys-Jones, Peter Colston, Michael Walters, Mark Adams, Cyril Walker) and the American Museum of Natural History in New York (George Barrowclough, Mary LeCroy, Paul Sweet, Allison Andors, Maria Rios), and also extremely important for the present volume have been the Louisiana State University Museum of Natural Science (Van Remsen, Steve Cardiff) and the Colección Phelps de Venezuela (Miguel Lentino); we are most grateful for all the help we have received at these institutions. We should also like to extend our particular thanks to the Field Museum in Chicago (David Willard), the Museum of Comparative Zoology in Harvard (Alison Pirie, Ernst Mayr, Raymond Paynter), the National Museums of Scotland in Edinburgh (Bob McGowan), the Sociedad Audubon de Venezuela (Clemencia Rodner, Mary Lou Goodwin, David Ascanio), the Natuurhistorisch Museum at Leiden (René Dekker), Liverpool Museum (Tony Parker), the Royal Museum of Central Africa at Tervuren in Belgium (Michel Louette), the University of Kansas Natural History Museum (Andrew Townsend Peterson) and the Natural History Museum of Los Angeles County (Kimball Garrett). We are particularly grateful to Peter Alden, who put himself to considerable trouble in order to take important photos for us at the Harvard collection.

Once again many libraries have made very important contributions to the volume. We should like to make special mention of Effie Warr of the British Museum of Natural History at Tring for her kind assistance throughout, in searching out countless papers and checking many references for us. We are also much indebted to the Museu de Zoologia of Barcelona (María Angeles Iglesias), the Sociedad Española de Ornitología in Madrid (Blas Molina) and the Estación Biológica de Doñana (José Cabot). Assistance with bibliographical references was also gratefully received from Raül Aymí (Grup Català d'Anellament), Andrés Bosso (Asociación Ornitológica del Plata), Eugenio Coconier (AOP), Stephen Debus, Anne-Marie Hinds (*Birds of North America*), Manuel Plenge, Thane K. Pratt, Ian Rowley (*Emu*) and Walter H. Weber (*Bol. SAO*). The references of scientific descriptions once again presented a number of problems,

and in addition to the sterling work of our Consultant, Walter Bock, we should like to thank Murray Bruce, Normand David, Alan Knox, Mary LeCroy, Miguel Lentino and Van Remsen for their help.

The present volume has benefited greatly from the generous input of many individuals. We are extremely grateful to Pamela C. Rasmussen, who readily lent us a great deal of her own personal photographic material to help with the plates, furnished us with a wealth of advice and unpublished data, and also refereed texts, much of this in connection with the complicated assemblage of Old World *Otus* owls. Guy Tudor has very kindly continued to lend us large numbers of photographs from the collection he has amassed over the years, and we offer him our grateful thanks. Michael Walters most generously sent us a manuscript of his unpublished monograph on the family Trochilidae, and in addition checked several scientific references. Jon Fjeldså, René-Marie Lafontaine and Mark Robbins all very kindly sent us reference material and information about newly discovered owl taxa that they have been working on. Once again, we are much obliged to the Royal Australasian Ornithologists Union and the editor of HANZAB, Peter Higgins, for generously sending us an advance copy of the proofs of their recently published Handbook.

We should also like to offer our hearty thanks to those who helped in diverse ways, for instance by refereeing texts, giving advice, or providing us with useful information, much of it unpublished; we would particularly mention Peter Browne, Rob Clay, Charles T. Collins, Stephen Debus, Geoffrey Field, Phil Gregory, Farah Ishtiaq, Alan Kemp, Ben King, Manuel Marín, Juan Mazar Barnett, Christopher Perrins, David Snow and Yuan-Hsun Sun. For their very useful advice on some long-term aspects of the project, we are very grateful to Nigel Collar, Stephen Debus, Peter Higgins, Alan Poole, Ian Rowley, Barry Taylor and Mike Wilson.

We are indeed fortunate to be able to continue benefiting from our agreements with VIREO at the Academy of Natural Sciences in Philadelphia (Doug Wechsler), and with the National Sound Archive of the British Library (Richard Ranft). We are also very grateful to Paul Coopmans, Rose Ann Rowlett (Field Guides) and Barry Walker (Manu Expeditions), who freely provided much information to help us in the planning of some projected fieldwork. Considerable efforts have been made to include the maximum information possible in the credits of each photo, and in this process agencies and individual photographers alike have been most co-operative.

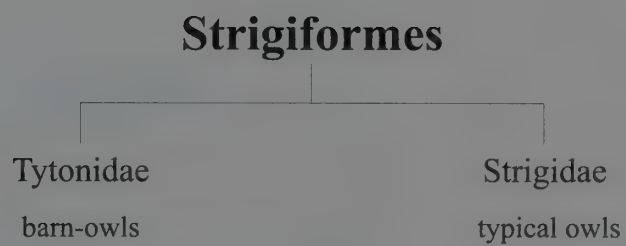
The various authors and artists involved in the volume would like to thank many of the institutions already listed above, but also the Academy of Natural Sciences in Philadelphia, the Library of the Australian Museum in Sydney, the Museu Paraense Emílio Goeldi, the New Forest Owl Sanctuary (Bruce Berry) and the Vogelpark Walsrode (Dieter Rinke). Their grateful thanks also go to Mark Adams, David Agro, David Alker, Pepe Álvarez, Allison Andors, J. Phillip Angle, Luiz dos Anjos, Mick Bagley, Richard C. Banks, Luis F. Baptista, Peter-René Becker, B. M. Beehler, Bob Behrstock, Emma Bennet, M. L. Birch, Walter Bock, Walter Boles, Jon Braggs, Wolf W. Brehm, Heike Brieschke, R. M. Brigham, Dan Brooks, Robb Brumfield, Jon Cantelo, Steve W. Cardiff, Becky Chantler, Elaine Chantler, Heather Chantler, Jack Chantler, Carla Cicero, Tony Clarke, Rob Clay, Brian Coates, Nigel Collar, Charles T. Collins, Joanne Cooper, Paul Coopmans, René Corado, Stephen Debus, René Dekker, Ron Demey, Kenneth P. Dial, Rod Elgar, Gonçalo Elias, Peter English, Lincoln Fishpool, Sylke Frahnert, C. B. Frith, Kimball Garrett, Luiz Gonzaga, Gary Graves, Suzanna Greenland, Ralph J. Guitierrez, Jürgen Haffer, David Hall, Andy Hanby, Anne Hawker, Richard Heading, Christopher Helm, Sebastian Herzog, Gene K. Hess, Janet G. Hinshaw, Ian Hodgson, David Hollands, Hans Hudde, H. D. Jackson, Olaf Jahn, Nigel Jarman, Ned Johnson, Scott Johnston, Leo Joseph, Allan Keith, Elisabeth Kietzmann, Lloyd Kiff, Andrea Klug, Claus König, Katja Kunz, Mathieu Lecorre, Mary LeCroy, Marlies Leutfeld, Bradley C. Livezey, Skye Loyd, Denize Machado, Alberto Madroño, Sjoerd Mayer, Gerald Mayr, Ian McAllan, Tony Mobbs, Cécile Mourer-Chauviré, Eberhard Mussler, K. Naoki, Clas M. Naumann, B. Nicolai, John O'Neill, Storrs L. Olson, David Oren, Gertrud Osten, Fernando Pacheco, Raymond A. Paynter, Lothar Peikert, Christopher Perrins, Dieter Stefan Peters, Alison Pirie, Doug Pratt, Thane K. Pratt, Roland Prinzinger, Robert Prys-Jones, Pamela C. Rasmussen, Nigel Redman, Josef H. Reichholf, Van Remsen, Swen C. Renner, Robert Ridgely, Mark B. Robbins, Ian Rowley, Phil Rye, Paul Salaman, Julio Sánchez, Marcela Santamaria, Kathrin M. Schuchmann, Gertrud Schuchmann-Wegert, Tom Schulenberg, Colin Shawyer, Adrian Skerret, Alexander Skutch, D. Smith, Gary Stiles, Becky Stoneham, Doug Stotz, Ewa Szpala, Mike Tarburton, Don Taylor, Ulrich Tigges, Angela Turner, Armando Valdés-Velásquez, Géraldine Veron, François Vuilleumier, Cyril Walker, Michael Walters, Effie Warr, David Wege, C. M. White, Bret Whitney, Andrew Whittaker, David E. Willard, Nicholas Williams, Raffael Winkler, Manfred Wittmann, Ulrike Wittmann, Dillon Wrathall and Kristof Zyskowski. The author of Caprimulgidae would like to

reiterate his thanks to all those listed on pages 11-12 of his recent monograph, Cleere (1998).

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Sadly, one of the authors of the present volume, Betsy Trent Thomas, died some time before its publication. Betsy was author of two families in Volume 3, as well as the one in Volume 5, and she had already started work on another for Volume 6. In our correspondence, she was always most enthusiastic and encouraging about the series; we are very sorry she did not live to see its completion.

Order STRIGIFORMES



Class AVES
Order STRIGIFORMES
Family TYTONIDAE (BARN-OWLS)



- Large-headed owls with heart-shaped facial disc, long legs and strong feet, usually with well-developed talons; plumage generally brown through buff and cream to white, spotted, speckled or barred.
- 23-57 cm.



- Almost cosmopolitan.
- Wide variety of habitats, from dense forest to desert, as well as urban landscapes and towns; from cool temperate zone to tropics, and from sea-level up to c. 4000 m.
- 2 genera, 16 species, 63 taxa.
- 5 species threatened; none extinct since 1600.

Systematics

For over two centuries, taxonomists have debated whether owls should be considered closely related to diurnal birds of prey (Falconiformes) or to nightjars and their allies (Caprimulgiformes). The hooked bill for tearing flesh and the strong feet and claws for capturing prey were significant in aligning owls to birds of prey, while their larger eyes, soft plumage and other adaptations to nocturnal hunting put them closer to caprimulgiforms. Yet, while now long accepted as being closer to the Caprimulgiformes and usually placed near this order, the evidence so far is not absolutely conclusive.

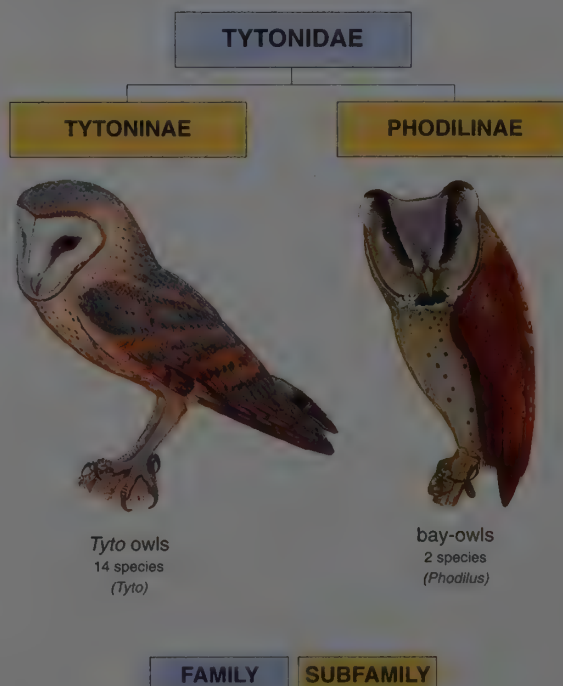
The review of owl classification by C. G. Sibley and J. E. Ahlquist in their 1990 work on DNA-DNA hybridization demonstrated this shift in opinion towards closer affinities with the Caprimulgiformes since the work of M. Fürbringer, H. von Gadow and F. E. Beddard in the late nineteenth century. Sibley and Ahlquist concluded their studies by combining the Caprimulgiformes with the owls in an expanded Strigiformes. In contrast, subsequent studies, including a report on allozyme divergence by E. Randi and colleagues in 1991, supported the traditional separation of Strigiformes from Caprimulgiformes.

A better understanding of the evolution and diversity of owls has emerged from the fossil record during the late 1980's and 1990's. At least six families are recognized, dating back to the Paleocene, up to 65 million years ago, with a major radiation taking place at least by the Eocene. From the Eocene, Oligocene and Lower Miocene deposits at Phosphorites du Quercy, in France, C. Mourer-Chauviré reviewed available material in 1987 and recorded two (later three) families. Tytonidae is represented by five genera and nine species: *Necrobyas* with five species; and four monotypic genera, namely *Nocturnavis*, *Palaeobyas*, *Palaeotyto* and *Selenornis*. *Palaeoglaux*, included with Tytonidae in 1987, was separated as *Palaeoglaucidae* when an additional species was described from Germany in 1992 and considered to show a mix of tytonid and strigid characters, as was the new family *Sophiornithidae* in 1987.

The diversity of Tytonidae in the Paleogene epochs (Paleocene, Eocene, Oligocene) is notable. With strigid owls first recorded in the Lower Miocene of Europe and North America, the evidence suggests that, along with the Tertiary radiation of small mammals, the diversification of owls increased through the Neogene epochs (Miocene, Pliocene), but with Strigidae generally superseding Tytonidae. The Quercy material represents two

extinct subfamilies of Tytonidae, *Necrobyinae* and *Selenornithinae*, sharing characters found in both *Tyto* and *Phodilus*. The genus *Necrobyas* is likened to *Tyto*, but with shorter and heavier legs. A succession of four of the species of *Necrobyas*, *N. rossignoli*, *N. harpax*, *N. edwardsi* and *N. arvernensis*, is represented from the Upper Eocene to the Lower Miocene, with an increase in size and a lengthening of the tarsometatarsus.

The genus *Tyto* dates at least to the Middle Miocene, with most of the dozen or so fossil species found in Pleistocene or Recent (Holocene) sites. The Common Barn-owl (*Tyto alba*) is known from sites dating back to the Pleistocene in Europe, Israel, and North and South America; the Ashy-faced Owl (*Tyto glaucops*) from Recent sites in the Dominican Republic; and possibly the Manus Masked-owl (*Tyto manusi*), or the Australian Masked-owl (*Tyto novaehollandiae*), or an undescribed species,



Subdivision of the Tytonidae

[Figure: Mark Hulme]



The classic feature of a barn-owl is its unique heart-shaped facial disc. This is possessed by all members of the family and instantly separates them from the "true owls" of the family Strigidae. The genus *Tyto* shows this character fully, the disc being very obvious and its shape almost perfectly that of a heart. The facial disc of the two *Phodilus* species is less markedly heart-shaped but is, nevertheless, highly distinctive.

[*Tyto alba alba*,
Perthshire, Scotland.
Photo: Neil McIntyre/
Planet Earth]

from Recent sites in the Bismarck Archipelago, off north-east New Guinea. Two sites have demonstrated an insular radiation of three size classes: the late Miocene of the Gargano Peninsula, Italy, formerly separated from the mainland, with *T. sanctialbani*, *T. robusta* and *T. gigantea*; and the late Pleistocene of Cuba, with *T. alba*, *T. noeli* and *T. riveroi*. In each case the first is the size of the extant Common Barn-owl, the second much larger, and the third gigantic. These size classes correlate with gigantism of mammals on islands, notably Cuba, where other giant fossil raptors are known, including a giant strigid owl. Fossil *Tyto* species elsewhere are generally much larger than the Common Barn-owl, for example *T. balearica* of Pliocene and Recent sites in Spain and France, *T. pollens* from the late Pleistocene of the Bahamas, and *T. ostologa* from the late Pleistocene of Haiti. In fact, *T. pollens*, *T. ostologa* and *T. noeli* appear to have been closely related insular counterparts. The Recent *T. cavatica* of Puerto Rico is probably closely related to the Ashy-faced Owl, and together these two represent part of an earlier radiation of taxa allied to the Common Barn-owl. *T. letocarti* from a Recent New Caledonian cave site may be generically separable from *Tyto*. However, fossil material from the Mascarene Islands that was formerly attributed to an extinct *Tyto* species is now considered to be unrelated.

The recent work on fossil material is further support for the division of living owls between the families Tytonidae and Strigidae, with the bay-owls (*Phodilus*) best placed with Tytonidae, though forming a distinct subfamily, Phodilinae. The separation of *Tyto* and *Phodilus* from other owls began in 1840 with the pterylographic studies of C. L. Nitzsch, who combined both forms in his genus *Hybris*. However, while separation of *Tyto* species as a family or subfamily has seldom been in doubt, the position of *Phodilus* has been open to question. Both F. E. Beddard in 1890 and W. P. Pycraft in 1903 considered *Phodilus* to be nearer to strigid owls, based on pterylography, osteology and other characters. A study of the syrinx in 1965 by A. Miller also considered *Phodilus* to be nearer Strigidae and not intermediate. In 1966, J. T. Marshall reviewed data on the skeleton, syrinx, voice, facial disc, ectoparasites and behaviour of *Phodilus*. He considered these characters to show departures from both Strigidae and Tytonidae without being clearly intermediate, and proposed recognition of a separate family, Phodilidae. The trend

of subsequent studies, ranging from behaviour to karyotypes, DNA-DNA hybridization and allozyme divergence, among others, is to support a Tytonidae family including *Phodilus*. By contrast, in a 1977 study of the evolution of bilateral ear asymmetry, R. A. Norberg supported the separation of *Tyto* from other owls but was uncertain about its affinity to *Phodilus*, and he considered their ear characters to have evolved independently.

Diagnostic characters of Tytonidae include a conspicuous facial ruff forming a heart-shaped disc, complete in *Tyto*, incomplete on the forehead and neck in *Phodilus*; an elongated and compressed bill; long legs, with feathers on the posterior side of the tarsus pointing upwards (*Tyto*) and feathered throughout (*Phodilus*); the inner toe as long as the middle toe, with the claw of the latter pectinated; the tenth, outermost, primary as long as the ninth; and the tail emarginated. However, while the family character of a pectinated or serrated middle claw is considered diagnostic, it has been reported as being absent from some specimens of *Phodilus* and in some specimens of at least one taxon of *Tyto*, namely the southern Andaman race *deroeptstorffi* of the Common Barn-owl.

In 1875, R. B. Sharpe recognized only five species of *Tyto* in the second volume of the British Museum Catalogue of Birds. This was quite extraordinary in an era when a large number of species were often recognized. A year later, however, in 1876, Sharpe explained this treatment by publishing his notes on his revision to highlight the considerable variation known for, in particular, the Common Barn-owl. He also included *Phodilus* with Tytonidae.

In the most recent full revision of *Tyto*, by E. Hartert in 1929, Sharpe's treatment was considered to be neither consistent nor logical. Hartert's review of the Common Barn-owl has been the basis for subsequent treatments, with only a few subspecies no longer recognized. His review of the Eastern Grass-owl (*Tyto longimembris*) was tentative and was clarified in later reviews by D. Amadon, who additionally combined this form with the African Grass-owl (*Tyto capensis*) in a single species.

Fourteen species of *Tyto* and two of *Phodilus* are currently recognized. Within *Tyto* the number of species has often been quoted as around eight to ten, but more species are now generally accepted. *Tyto* is represented by four groups: sooty-owls (two species); masked-owls (six); typical barn-owls (four); and grass-



With its very wide, virtually cosmopolitan distribution, it is hardly surprising that the Common Barn-owl has evolved a large number of subspecies. Some of these may merit full specific treatment.

The Galapagos subspecies, although distinctive enough, has not yet been elevated to that status. On the other hand, the Ashy-faced Owl, until relatively recently considered conspecific with the Common Barn-owl, is now generally afforded full species status.

[Left: *Tyto alba punctatissima*, Santa Cruz, Galapagos Islands. Photo: Robert Behrstock/VIREO.

Right: *Tyto glaucops*, Santo Domingo Zoo, Dominican Republic. Photo: Josep del Hoyo/Lynx]

owls (two). The greatest diversity of species is found in Australia, New Guinea and islands west to Sulawesi, including all the sooty-owls and masked-owls. The typical barn-owls and grass-owls overlap in parts of southern Asia west to India and in Africa south of the Sahara. Elsewhere, only the typical barn-owls occur.

It is thought that the masked-owl group along with the sooty-owls may be relicts of an ancient radiation which subsequently contracted, leaving behind isolated representatives in Wallacea, Melanesia and Australia. Later, though still in ancient times, the typical barn-owls and the grass-owls would have resulted from another more far-reaching radiation, with separate centres of speciation, for example in the West Indies.

The sooty-owls number two species. In the early 1980's it was proposed that the Lesser Sooty-owl (*Tyto multipunctata*) of north-east Australia should be separated from the Greater Sooty-owl (*Tyto tenebricosa*) of south-east Australia and New Guinea, on the basis mainly of differences in size, plumage and voice. While this creates an unusual distribution pattern, it is shared by at least one other bird genus, that of the logrunners, *Orthonyx*. There has been much recent work on Australian populations of these owls, but New Guinean birds remain poorly known. While most authors now accept the split into two species, some consider the New Guinea populations to be equally distinctive, which could imply their promotion as a further species, although others might use this instead to call for the regrouping of all forms into a single species once again.

The masked-owl group is currently considered to comprise six species, including several isolated and poorly known island endemics. The Australian Masked-owl occurs widely in Australia and also in southern New Guinea. North-east of New Guinea are found the Golden Masked-owl (*Tyto aurantia*) on New Britain and the Manus Masked-owl in the Admiralty Islands. West of New Guinea are the Lesser Masked-owl (*Tyto sororcula*) of the Tanimbar Islands, Buru and Seram; the Taliabu Masked-owl (*Tyto nigrobrunnea*) of the Sula Islands; and the Minahassa Masked-owl (*Tyto inexpectata*) of northern Sulawesi. However, the taxonomic status of many forms within this group is far from clear. All six are currently placed in a single superspecies, and until quite recently many of them were frequently considered races of a single more widespread species. Again, the Taliabu and Minahassa Masked-owls are occasionally considered conspecific; the fact that the former is known only from a single specimen, together with recent field observations, means that it is very

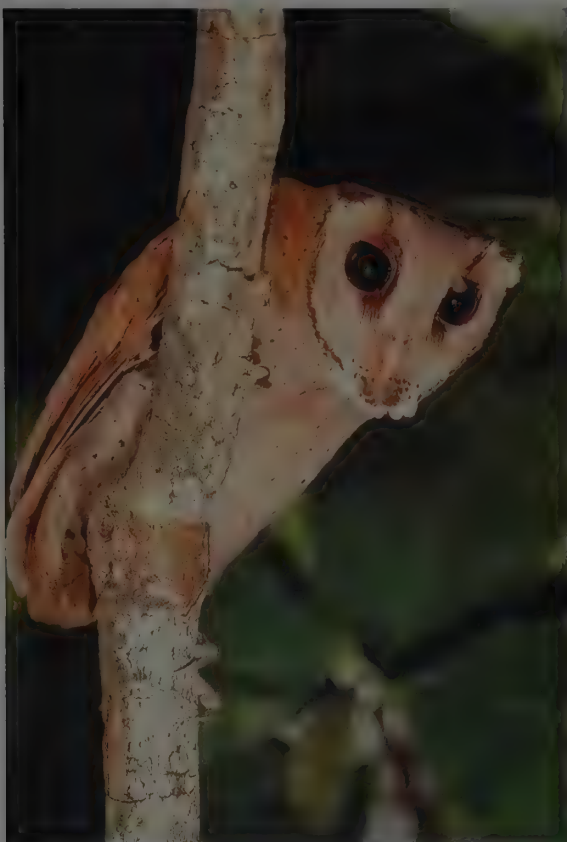
difficult to make meaningful assessments, and indeed there are those who might instead make this form conspecific with the Australian Masked-owl. At the other end of the scale, the large, dark Tasmanian form *castanops* of the Australian Masked-owl is frequently considered a full species in its own right, although recent studies suggest that its differences from the closest mainland populations of nominate *novaeollandiae* are probably best reflected as subspecific. It has also been suggested that the Australian Masked-owl's form *calabyi* from southern New Guinea might be approaching separate species status, although this proposal has received little support. As in the case of the sooty-owls, this New Guinea form is very similar to the southern Australian nominate race, but less so to the geographically much closer north Australian races, though even in this latter zone the differences would appear relatively slight, especially within the context of this very variable species. A further dubious case within this group is that of the form *cayelii* of the Lesser Masked-owl, which occurs on Buru and Seram. This taxon may represent another separate species from the Tanimbar form, *sororcula*, while the Seram population may involve a separate race yet to be described. All in all, there are a great many uncertainties within the masked-owl group. Apart from recent studies of Australian birds, the group is very poorly known and includes some of the least-known owls in the world.

By contrast, the Common Barn-owl has the distinction of being one of the world's most widely distributed landbirds, as well as the most intensively studied of all owls, particularly in Europe and North America. However, of the 28 subspecies presently recognized, most are poorly known, and some isolated populations may represent separate species. This has proved to be the case for the Ashy-faced Owl of Hispaniola, now separated from the Common Barn-owl, and reckoned probably to include the dark barn-owls of the Lesser Antilles, although these might represent a further species, *T. insularis*. Other isolated island forms that might merit promotion to full species include the current races *detorta* of the Cape Verde Islands, *thomensis* of São Tomé, *deroepstorffi* of the southern Andamans, and *punctatissima* of the Galapagos. Interestingly, birds from both the North American race *pratincta* and the Australian race *delicatula* were introduced to Lord Howe Island, off north-eastern Australia, and declined to interbreed; this was taken as evidence that the two taxa should not be considered to belong to the same species. However, further investigation was cut short, as

The two sooty-owls were long regarded as representing a single species. Their present treatment, as separate species forming a superspecies, is based on differences in size and plumage, as well as in voice. A glance at their individual distributions may cause some surprise, however, since the Greater Sooty-owl is found in New Guinea and in south-eastern Australia, while the area between those two regions is occupied by the other species, the Lesser Sooty-owl (*Tyto multipunctata*). The situation is further complicated by the fact that the New Guinea population, although still poorly known, is sometimes thought to be distinctive enough as to represent a third species; other taxonomists may feel that, if New Guinea birds are that different, then this could support the argument for re-merging all sooty-owl populations into a single species comprising several well-marked subspecies. Clearly, there is a need for much more study of this group of attractive birds, particularly at the extremes of the range.

[*Tyto tenebricosa arfaki*,
New Guinea.
Photo: Len Robinson/
FLPA]





both forms went extinct on the island, leaving possible conclusions in the air. The two other members of the group of typical barn-owls are poorly known but very distinctive island endemics: the dark-backed Sulawesi Owl (*Tyto rosenbergii*) of Sulawesi, Sangehe and Peleng, which has also been allied with the masked-owls; and the Madagascar Red Owl (*Tyto soumagnei*) of eastern Madagascar.

Grass-owls are commonly treated as two species, although they are still often combined as one. Despite the disjunct range that is produced by such a "lump", morphological differences between the two forms are minimal, while subspecific variation within the Eastern Grass-owl is notable, so the case in favour of splitting is by no means overwhelming. The African Grass-owl has been the subject of various studies, particularly in South Africa. The rarity of the Eastern Grass-owl through much of its range has limited the amount of information available on it, but recent work in Australia has begun to fill some of these gaps.

What little is known about the two bay-owls of the genus *Phodilus* tends to support their inclusion in Tytonidae as a distinctive subfamily of isolated, relict populations. The Oriental Bay-owl (*Phodilus badius*) ranges extensively through South-east Asia, but is considered very rare throughout its range. What is known of it in life is limited to random observations over many years on voice, behaviour, nest-sites and eggs, with no other details of breeding. Even this is considerable when compared with our knowledge of the Congo Bay-owl (*Phodilus prigoginei*), a remarkable species discovered in Africa as recently as in 1951. The type specimen, a female, was the sole definite source of information until another female was mist-netted and released at the same locality in 1996, though there were two probable records from the intervening period. In the past, it was strongly argued that the Congo Bay-owl should really be treated merely as a race of the Oriental Bay-owl, as it was said to be virtually identical. Although little new information of note has been unearthed, it is now generally agreed that the differences are a good deal more marked than previously suggested, and indeed the two may not even be congeneric.

Some nomenclatural confusion has concerned tytonid owls in the past owing to problems over the application of the Linnaean

genus *Strix*. Prior to 1910 the *Tyto* owls were placed in *Strix* or its synonyms, such as *Aluco*, until G. M. Mathews called attention to the availability of *Tyto*. Within the typical strigid owls, *Strix* replaced *Syrnium*, with *Strix aluco* as its type. The Common Barn-owl had been most widely known as *Strix flammea* and its family as Strigidae, while all other owls were placed in Bubonidae or Asionidae, so name changes were required. At the species level, too, changes in nomenclature have proved necessary. For example, the Eastern Grass-owl was long known as *Strix candida* until Mathews at the same time demonstrated the unavailability of *candida* and the application of *longimembris*.

Morphological Aspects

Owls of the genus *Tyto* have a large, rounded head with a heart-shaped facial disc, a narrowly tapering body with a short, squared tail, long legs, and strong feet with well-developed talons. In flight, the blunt-headed shape makes them appear top-heavy, with long wings and long, often trailing, legs. The exceptions are forest-adapted forms with rounder wings for flight among trees, and smaller forms with less robust feet and talons. The longer legs are more prominent in forms inhabiting open country.

Tyto owls are characteristically darker on the upperparts, with variable markings, and paler on the underparts, with or without markings. The palest forms, of temperate and arid regions, are light grey with some buff or golden-yellow wash on the upperparts, which are delicately marked in intricate patterns of white, grey and black, while their white underparts are either unmarked or have dark flecks or spots, these often confined to the sides of the breast and belly. The darkest forms are dark brown or black, with the underparts only slightly paler, and are also intricately patterned above and spotted or flecked below. Many variations are found between these extremes. The markings may be apparently random or may form loose vermiculations or barring, but never the heavy streaking shown by many of the Strigidae. Overall, the effect is cryptic and serves to camouflage hunting and roosting birds against predation from above; the paler underparts of many species contrast less with the sky when seen by prey from below, while the darker forms blend with their darker backgrounds, such as forest or lava rock, as in the Galapagos. Some forms occur in light, intermediate and dark colour morphs, and the ratio of light to dark is also a reflection of habitat adaptations generally. Such influences of habitat and hunting behaviour have not only made these owls well adapted to their environments, but, in the case of the Common Barn-owl, have resulted in a diversity of races with similar plumage patterns in different regions of the world. These variations and convergences explain the difficulty faced by R. B. Sharpe in the nineteenth century in defining species limits (see Systematics).

As a rule, females are larger and darker than males, and the degree of difference may be considerable. In many forms the generally paler appearance of the males is considered to be advantageous, as males do most of the hunting during the breeding periods. Females tend to have larger and darker spots on the wings and tail, giving a barred effect, and larger and more numerous dark spots or flecks on the underparts.

Newly fledged young of both sexes are generally darker than their parents until after the first moult, when breeding age is reached. Females become paler with age, and older females may approach paler males in colour. They are heavier than males and their weight fluctuates throughout the breeding period, while males tend to be of a similar weight all year around. The lightest birds are found among races of the Common Barn-owl, with a weight of as little as 187 g recorded, while the heaviest are the dark females of the Tasmanian race of the Australian Masked-owl, which weigh up to 1260 g. The latter are also the largest tytonids, at 57 cm long, whereas some races of the Common Barn-owl and some other taxa are as small as 26 cm, and Oriental Bay-owls can measure only 23 cm. Size differences within species, sometimes combined with plumage differences, have been used to define racial variation, but there can be much individual variation in widespread populations, while small size is more constant in smaller populations, such as those on islands.

Owing to their rarity, the bay-owls are very little known. Of the two species, the Oriental Bay-owl has the wider distribution and has been better studied. Its relationship with the genus *Tyto* is perhaps debatable, but on current evidence its inclusion as a subfamily within the Tytonidae appears to be warranted. By contrast, treatment of the virtually unknown Congo Bay-owl (*Phodilus prigoginei*) as a subspecies of the Oriental, as was formerly argued, is surely untenable: indeed, to judge from its external appearance, the African species seems unlikely even to be congeneric with the Oriental Bay-owl.

[*Phodilus badius badius*, Malaysia.
Photo: Graham M. Lenton/
Aquila]

Their characteristic pattern and coloration makes barn-owls instantly identifiable, both to the professional and to the layman. The typical plumage, as shown by this Common Barn-owl, is dark above, with a variable amount of golden-buff and with a delicate spotting and flecking of grey, white and black; the underparts are much paler, often whitish, with or without dark spots. Cryptic plumage of this kind is found among many birds, although one may wonder about the effect of such pale underparts for a bird which does much of its hunting in the darkness of night.

[*Tyto alba pratincola*,
foothills of Rocky
Mountains,
Colorado, USA.
Photo: François Gohier/
Auscape]



Tyto owls are supremely adapted to nocturnal hunting. The facial disc is formed by layers of stiff, dense feathers which act as reflectors amplifying sounds, including high frequencies. The heart shape of the disc forms two concave troughs running along the sides of the face. The asymmetrical positions of the external ears allow the owls to determine the location of sounds. The left ear is higher than the right one and so, when the owl turns its face towards the sound source, the orientation of the disc is slightly downward on the right and upward on the left. By comparing the extremely fine differences in the timing of the sounds in both ears, the owl can determine the direction of the noise of potential prey, as well as distinguish prey sounds from other sounds, such as rustling leaves. The owl can also locate concealed prey, such as in grass or under snow. The optimum foraging height appears to be around 3 m, either when hunting or when preparing to strike. While it has been demonstrated that Common Barn-owls can hunt in what appears to the human eye to be complete darkness, they also hunt visually in variable light conditions at night and early or late in the day, for instance in the tropics; or for more extended periods, such as during the long days of summer at high latitudes. The degree of nocturnal hunting is also indicated by eye size, the sooty-owls, which are also known to hunt in complete darkness, having the largest eyes.

The silent flight of these owls reduces the chance of audible detection by small mammal prey and helps them locate prey sounds when hunting from the air. Three adaptations of the flight-feathers assist in providing this silent flight. First, the leading edges, particularly of the outer primaries, have a prominent, stiff, comb-like fringe, providing a laminar air flow that reduces noise; second, the trailing edges of the primaries and secondaries have a soft, hair-like fringe that helps to reduce turbulence where the air flows across both sides of the wings meet; and last, the primaries, secondaries and wing-coverts have a downy surface that reduces the noise made by their contact during wingbeats. The wings are also broad, giving a high surface-area to body-mass ratio which increases lift and allows slow flight and sudden turns without stalling. The low wing-loading also allows heavy prey to be carried at slow speed, thus reducing the power output required and minimizing energy consumption, which is advantageous when prey is being delivered frequently to the nest. Such flight movements when hunting, combined with long, slender legs and large

toes and claws giving a wide spread at points of contact, make these owls efficient hunters in a variety of habitats.

Bay-owls are like small dark *Tyto* forms, but with the facial disc divided at the forehead and forming ear-like extensions of the ruff margin of the disc, which is less complete above the neck. Their general appearance is that of small forest owls superficially resembling their *Tyto* counterparts, the sooty-owls, and in particular the smaller, tropical Lesser Sooty-owl. All taxa of bay-owl are dark, variably brownish, and more heavily marked on the upperparts, while they are more uniformly coloured and slightly paler on the underparts, a pattern in which they resemble the *Tyto* owls to a fair degree.

Studies of the moult of the Common Barn-owl have demonstrated a complex sequence that differs from that of strigid owls,

The distinctive outline of *Tyto* owls in flight is well demonstrated by this African Grass-owl. The large head makes the bird appear markedly front-heavy, and the relatively long legs protrude noticeably beyond the short, square-ended tail. The legs are particularly long in those species living in open country, as do the two grass-owls. This individual, flushed from its regular daytime roost in rank Imperata grass in an extensive marshy area, is a subadult, aged by the more buffy colour of its underparts.

[*Tyto capensis*,
Nyl River floodplain,
South Africa.
Photo: Warwick Tarboton]





can be determined after fledging by the sequence of moult of the primaries. The first moult usually replaces the central P6 only, the second moult usually 2-4 primaries either side of P6, and the third moult renews the remainder. Subsequent moults usually see the primaries, still centred on P6, replaced every two years. The secondaries and the tail feathers are also not completely replaced until after the first three moult phases. While tropical birds replace all wing and tail feathers over about seven months, the sequence is similar to the temperate three-moult sequence. Outer primaries are usually replaced rapidly, while the inner primaries and secondaries are renewed over a longer period. The timing of moult is strongly influenced by food supply and extends over the entire breeding period. In years when prey numbers are low the moult phases are slower.

Habitat

Tytonidae is essentially a tropical family that ranges into higher latitudes. Most species are confined to tropical forest and some adjacent habitats from the coast up to and beyond the tree-line, reaching about 4000 m in the Andes and New Guinea.

Both sooty-owls are rainforest specialists. In south-east Australia, the Greater Sooty-owl prefers old-growth forest, often wet gulley forest, dominated by tall eucalypts, with creeks and a dense understorey of smaller trees and ferns. Although also extending into drier forests to hunt, it is sensitive to disturbance and its presence is a good indicator of the biodiversity in a given habitat. In New Guinea, the species ranges to about 4000 m above sea-level and is also found in *Araucaria* pine forest. It sometimes hunts above the tree-line in boulder-strewn alpine grassland and along ridges, as well as in clearings at lower elevations. Within its much smaller range, the Lesser Sooty-owl shows a similar preference for pristine forest, usually occurring in clearings and disturbed areas only for the purposes of foraging.

The tropical masked-owls are all restricted to lowland and mid-montane rainforest, but they may occur at the forest edge and in adjacent lightly disturbed habitats when hunting. The Australian Masked-owl occurs widely in all forest habitats, preferring tall open forest with large trees for nesting and roosting and a diverse understorey with ground cover for hunting. Inland, its

The silent flight of tytonid owls is aided by several special adaptations. One of these is the stiff, comb-like fringe at the leading edges of the flight feathers, especially the outer primaries, visible on this Madagascar Red Owl as it stretches its wing. This produces a laminar flow of air across the wing, helping to reduce noise. The facial disc is composed of layers of stiff, dense feathers which amplify sounds, thereby further facilitating nocturnal hunting. The orange-red plumage gives this very rare species its vernacular name. This individual, perched 27 m up on a large trunk, is one of the sole pair to have been studied to date.

[*Tyto soumagnei*, near Ambanizana, Masoala Peninsula, north-east Madagascar. Photo: Russell Thorstrom]

providing further support for the separation of Tytonidae. However, while birds of temperate regions moult their juvenile set of remiges and rectrices over three moult phases from their second to their fourth years, followed by a two-year moult cycle, those inhabiting tropical regions apparently moult all their wing and tail feathers each year. The age of temperate Common Barn-owls



Sexual dimorphism is not particularly well marked in the Tytonidae. Females are generally larger and darker than males, and often have more spots on the underparts, but in many cases the sexes are distinguishable only by size. The Australian population of the Eastern Grass-owl, however, is a possible exception. Although it seems that some females of this largely terrestrial species are very similar to males, many have a noticeably darker facial disc and underparts. Juveniles either resemble females or are darker still.

[*Tyto longimembris longimembris*, Australia. Photo: Roland Seitre/Bios]

foraging habitats may extend to wooded farmland, tree-lined watercourses, pine plantations and isolated tree stands, and in northern Australia also paperbark (*Melaleuca*) swamps and mangrove edges. More remarkably, in the south of the continent one population has adapted to underground caves of the treeless Nullarbor Plain.

In contrast to the case of forest species, the habitat diversity of temperate populations of the Common Barn-owl is limited only by prey availability, by seasonality and the severity of winters at higher latitudes, and possibly by competition from other predators. This owl prefers lowlands with scattered tree cover, such as non-intensive farmland featuring hedges, ditches, ponds, banks, roadside verges and similar habitat mixes, young pine plantations, and villages, towns and suburbs with tree cover and unoccupied buildings suitable for daytime roosts and nest-sites. Tropical and subtropical races range from rainforest to the xerophytic vegetation communities of arid and semi-arid regions, including shrub and herb communities, mixed woodland, savanna, heath, marshland, mudflats, cliffs and rocky coasts, including some continental offshore islands. These races also occur in urban landscapes, as well as plantations, rice paddies, cane fields and irrigated fields. On smaller tropical islands Common Barn-owls enter all available habitats, although some races depend on areas of undisturbed rainforest for breeding.

While the tropical relatives of the Common Barn-owl, the Ashy-faced and Sulawesi Owls, are sometimes found in forest, they are more characteristic of open woodland, forest edge and cultivation, and also occur around villages and towns. Recent observations show that even the rare Madagascar Red Owl, hitherto known only as a resident of undisturbed rainforest, may be beginning to adapt to secondary-growth woodland with clearings.

Grass-owls occur widely in the Old World tropics and reach South Africa in the west and southern Australia in the east. The African Grass-owl, perhaps because of competition from the strigid Marsh Owl (*Asio capensis*) in particular, is generally restricted to undisturbed grassland at elevations of up to about 3200 m, marshes, *Acacia* woodland and floodplains, including vleis in South Africa. The Eastern Grass-owl is sparsely distributed through Asia to Australia in similar grassland, floodplains, savanna and marsh habitats up to about 2500 m. In Australia, it appears to break up into eastern coastal and inland populations,

never having established permanent breeding populations farther south than subtropical areas. It prefers undisturbed areas but is also found in cultivation, such as cane fields and young pine plantations, and in cleared areas. Inland grass-owl populations, as with many inland birds affected by the wet and dry seasonality of available habitat and food resources, are highly nomadic and can be locally common where several good wet seasons have resulted in high rodent populations. In subsequent drier conditions these inland birds disperse widely, with most apparently moving north to tropical savannas, marshes and swamps, and it has been suggested that the northern coastal populations may not be permanent but a consequence of deteriorating conditions for inland birds.

The bay-owls are both forest specialists, and the sooty-owls may be their ecological counterparts in Australia and New Guinea. The Oriental Bay-owl is found in lowland and mid-montane rainforest and mixed deciduous forest, but it also occurs at the edges of mangroves, and in plantations and old clearings, utilizing the clearings probably only when hunting. The little information available on the Congo Bay-owl indicates that it is a forest owl that also hunts in disturbed forest, clearings and probably plantations.

General Habits

Tytonid owls are, with few exceptions, strictly nocturnal. They occur solitarily or in pairs, and are generally sedentary birds occupying a territory throughout the year, which may or may not be defended outside the breeding period. Territory size varies with breeding and non-breeding activities and, particularly in temperate regions, with prey availability, quality of foraging habitat and prevailing weather conditions. The distribution and density of territories can at times be limited only by the availability of suitable nesting sites and roosts. Studies of the Common Barn-owl in Europe and North America show much variation in territory requirements, but where conditions for breeding are good the optimal number of pairs will establish and maintain territories. A similar maximum exploitation of suitable habitat has also been demonstrated for sooty-owls, grass-owls and the Australian Masked-owl. Sooty-owls and masked-owls are more strongly territorial than are typical barn-owls and grass-owls.

While most tytonids are forest-dwelling species that sometimes extend into adjacent habitats, the most widespread member of the family can be encountered in an extraordinary variety of habitats across its worldwide range. Tropical races of the Common Barn-owl can be found in rainforest and in xeric habitats, as well as in various types of woodland and grassland, in coastal regions and in semi-urban and even urban areas. Populations in temperate parts of the range prefer lowland areas with some tree cover, often farmland with hedges, banks and ditches, and with unoccupied buildings in which to roost and nest. Barns and outbuildings are frequently used.

[*Tyto alba alba*,
Ávila, Spain.

Photo: Francisco Márquez]





In contrast to the Common Barn-owl (*Tyto alba*), the two sooty-owls are habitat specialists, more or less confined to the rainforest of Australia and New Guinea. Their requirement for undisturbed and undegraded forest has meant that they are only infrequently recorded, and disturbance of the habitat leads to a decline in their numbers. The rarer of the two, the Lesser Sooty-owl, lives mostly at altitudes above 300 m and is seldom encountered outside the forest proper; it appears in clearings and in areas adjacent to the forest only to hunt.

[*Tyto multipunctata*, Paluma, Mt Spec-Crystal Creek National Park, north Queensland, Australia.
Photo: Clifford & Dawn Frith]

A high density of breeding pairs with overlapping territories in a few regions suggests loose colonies, and pairs may defend an area of only about 5-10 m around the nest. Territories are established by males and are sometimes occupied over several years. If one member of a pair dies, the other may continue to defend the territory or may re-establish itself in a new one, usually no more than a few kilometres away. A female has been recorded defending the same territory for nine years, but the mortality rate of adults means that most individual territories last only about two years. One of the effects of maintaining territories is that, if prey is scarce, some birds will starve rather than move to a more favourable area; another is that pairs may at times be found breeding close to the nest-sites of other owl species and raptors.

Resting owls hang their plumage loose and stand on one leg with the body leaning forwards, the facial disc flattened and the eyes closed. The plumage is often preened at this time in order to maintain peak feather condition for hunting. Other maintenance activities observed for the Common Barn-owl include bathing in a stream in sunny weather, as well as sunning by lying on a well-lit patch of ground and raising one wing to expose the side of the body to the sun. These activities may also help to control ectoparasites. If the owl is disturbed when roosting, it draws its body upright and holds its wings tight and partially wrapped around the body; for those species and subspecies which have pale underparts, this posture helps to conceal that conspicuous part of the plumage.

Common Barn-owls are sensitive to disturbance, and their threat displays are very similar to those that have been observed in other *Tyto* species. If threatened by an intruder, the owl bows towards the source of the threat and spreads its wings, tilting them forwards with the tail raised and spread; the head is lowered to show the nape and is swung from side to side, this action accompanied by hissing and bill-snapping. If cornered, the owl sways its lowered head and upper body from side to side while standing alternately on one foot then the other, ruffles its plumage, lowers its wings, and spreads its tail. The head is shaken and moved up and down while the bird glares at the source of danger, hissing with the bill open and making sudden forward lunges. If attacked or approached too closely, the owl may raise a foot,

lean backwards and strike forwards with its talons. The spraying of faeces at the source of threat has also been recorded. If the owl is then picked up, it may feign death, closing its eyes and lying prostrate. These displays vary, depending on the circumstances, and are not used against others of its own kind. Fledged young are bolder than adults and sometimes use such displays to mob mammalian predators.

The general habits of the bay-owls are almost unknown. The two species are strictly nocturnal and easily disorientated if found in daylight. A threat display of the Oriental Bay-owl observed in Malaysia exhibits similarities with that of *Tyto*. The owl stood up on stretched legs, turned towards the observers, inclined its body forwards, and arched its wings out and down to below the level of its toes. In this posture it swayed from side to side, then suddenly bowed its head deeply and shook it while facing nearly backwards between its own feet. For a few seconds it exposed its neck and nape, then the head was flung up and forwards to expose the pale facial disc with its large staring eyes and open bill. This sequence was repeated before the bird flew away. While some aspects of the threat display are found in some strigid owls, the bowing and shaking of the head is certainly characteristic of the Tytonidae.

Voice

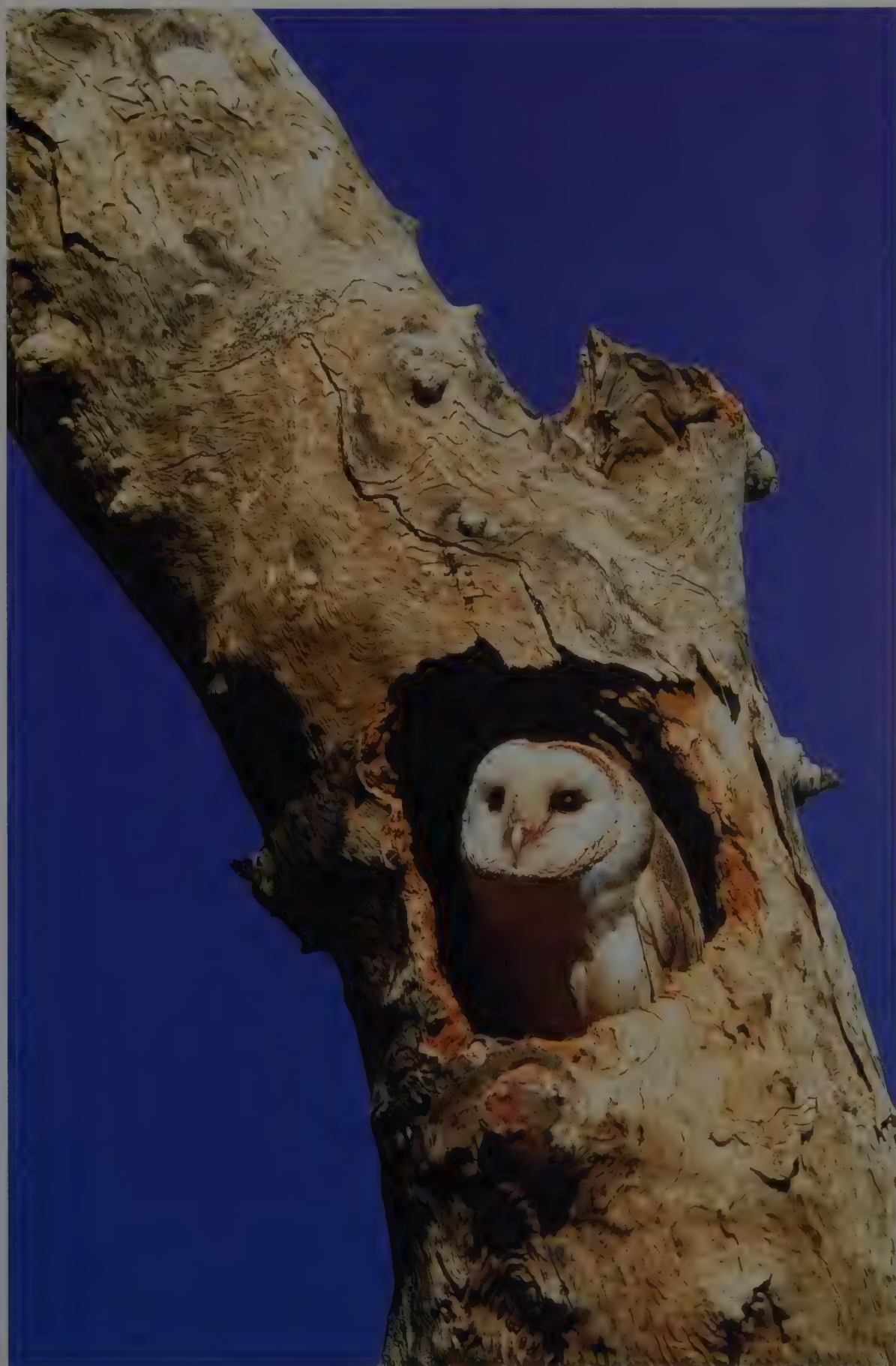
The voices of tytonid owls are characterized by various screeches, screams and shrieks, in addition to some chirruping and whistling sounds. A cacophony of cackles, chatters, chuckles, croaks, hisses, purrs, rasps, snores, squeaks, trills, twitters, wails, wheezes, yelps and even yodels is usually associated with breeding activities and variously uttered by males, females and their young in the nest and later near it.

In 1980 a German study by P. Bühler and W. Eppe summarized the calls of the Common Barn-owl, placing them in five groups. These are variations of the sounds listed above, in their different forms and combinations representing courtship, contact calls, pair-bonding, begging and feeding calls, and defensive and territorial behaviour. In 1982, the vocal repertoire of this species in England was categorized by D. S. Bunn and colleagues

In the arid, harsh interior of Australia, the Common Barn-owl is forced to retreat from the heat of the day by taking refuge in a suitably cool cavity. This species is, in fact, largely nocturnal, although, in many parts of its vast range, it is not uncommonly seen hunting at or just before dusk and around dawn; on occasion it even appears in the middle of the afternoon, especially if disturbed from its daytime roost. Common Barn-owls are often associated in people's minds with old, disused buildings, barns and similar artificial structures, but one of the most frequently used sites for roosting and nesting is a large natural cavity in a tree trunk. Such sites are adopted in all parts of this adaptable species' range, the main condition for its presence being not, as sometimes believed, the availability of old barns and the like, but an adequate supply of prey and, partly implicit in that, a winter climate that is not too severe. Competition from other predators can also be a factor in its occurrence or otherwise in apparently suitable areas.

[*Tyto alba delicatula*,
near Alice Springs,
Northern Territory,
Australia.

Photo: Jean-Paul Ferrero/
Auscape]





into at least 12 types of sound. In addition, this species is known to make mechanical sounds in the form of both Bill-snapping and Wing-clapping.

We also have some idea of the range of calls of the three other *Tyto* groups. They all have distinctive features in both vocal character and calling behaviour, but the types of call known so far suggest similarities with the Common Barn-owl. For example, grass-owls make cricket-like chirruping calls in flight, and sooty-owls give a characteristic piercing, descending whistle, likened to the sound of a bomb falling, while the Australian Masked-owl screams louder than other *Tyto* species within its range.

The voice of the Oriental Bay-owl is characterized by various screams and whistles, even a soft hoot. A well-known description of its scream was that it sounded like half a dozen cats fighting. The whistling calls include short, three-noted and longer, more musical sequences. One of the "probable" records of the Congo Bay-owl was of a bird uttering a structurally similar call.

Food and Feeding

As with so many other aspects, our knowledge of the diet of tytonid owls rests heavily with that of the Common Barn-owl, which has been studied in greater detail than any other owl. For seven other species we have a good idea of their diet, for three we know very little, and for five species we know nothing.

In general, tytonid owls are predators of small to medium-sized mammals, with birds, reptiles, frogs, insects and other prey of incidental, seasonal or local significance. The typical barn-owls and grass-owls are specialized hunters of small mammals, especially rodents and shrews (Soricidae), with voles (Cricetidae) of particular importance to temperate Common Barn-owl populations. Sooty- and masked-owls in Australia and New Guinea take a range of marsupials as a major part of their mammal diet. The Oriental Bay-owl appears also to be a hunter mainly of small mammals, although birds and other prey may be important, but nothing is known of the relative percentages of different prey and all available data remain anecdotal, as is the case, too, with the little-known *Tyto* species.

Pellet analysis has been the principal source of dietary data for the Common Barn-owl and other *Tyto* species so far studied. The Common Barn-owl's stomach is known to have a pH higher (less acidic) than that of most other predatory birds, with the result that even small, delicate bones may be found intact in its pellets. Not only does this ease identification of prey species, but also studies have found that the proportions of prey identified in pellets match other sources of data, such as food remains at nest-sites and photographic evidence of prey delivered to nests. However, a study in Mali found that, for some pairs that fed almost entirely on frogs and toads, the remains of such prey did not show in pellet analyses, which underestimated the importance of amphibians in the diet. A recent Israeli study of Common Barn-owl pellets aimed at determining the ecology and distribution of mammal prey suggests that the pellets do not represent the actual proportions of the available prey species in their real communities, but they do give an accurate indication of the owls' preferences, though showing a bias towards larger prey species, with most items identified falling in a weight range of 51-100 g.

The most recent major analysis of Common Barn-owl diets was that undertaken by I. R. Taylor in 1994. He combined the results of his 14-year Scottish study with 51 previously published reports selected on the basis of the length of study and the number of birds involved, also including shorter-term studies to give a broader geographical coverage. The representation is Europe (22), Middle East (1), Africa (7), North America (15), South America (2), South-east Asia (1) and Australia (4), which is also a good indication of the global ratio of all studies of Common Barn-owl populations.

Taylor found that the proportion (in terms of numbers) of small mammals in these 52 samples was 74-100%, making up over 90% in 42 cases. As a general rule, small mammals are most important in moist, temperate regions, the great majority being terrestrial species weighing 3-100 g, although in most studies

Wing-stretching is a commonly indulged-in habit among many birds of all families, and the Tytonidae is no exception. This behaviour helps to keep the plumage in good working order, and also ensures that the individual feathers are correctly aligned when the wing is folded again. Barn-owls, when perched, generally hold their plumage rather loose; if suddenly disturbed or alarmed in any way, however, they immediately draw the body upright and press the wings tightly against the sides. In such situations, the Common Barn-owl, and almost certainly its relatives as well, also wraps its wings partly around the front of the body, a posture which goes some way towards concealing the conspicuous pale underparts that would otherwise easily attract the attention of a potential enemy.

[*Tyto alba alba*, near Ringwood, Hampshire, England. Photo: Mike Read/Planet Earth]



One of the frequently practised maintenance activities recorded for barn-owls is demonstrated by this individual. Perched on a favourite post, with body leaning slightly forwards and plumage hanging loose, the owl stands on one leg and scratches its face with the other. This is part of the general preening routine that keeps the feathers in peak condition for hunting and helps to maintain general health.

The majority of birds are creatures of habit. This Common Barn-owl is one of a breeding pair which regularly used this particular post; every evening, the bird perched on it and preened for a short while before flying off to hunt. In this posture, and in such a close-range view, the golden-buff crown with its wonderfully delicate pattern of dark dots superimposed on a light grey veil-like bloom is revealed to advantage.

[*Tyto alba alba*,
near Ringwood,
Hampshire, England.
Photo: Mike Read/
Planet Earth]



Any intrusion near the nest of a barn-owl is likely to elicit the distinctive defensive or threat posture that so characterizes the Tytonidae. The spread-wing posture is typical, having the effect of making the bird appear bigger than it actually is. The bird first bows in the direction of the intruder and spreads its wings wide, at the same time turning them forwards so that their upper surface faces the source of the threat, and raises and spreads its tail; it lowers its head and swings it from side to side, while uttering hissing sounds and snapping with the bill.

[*Tyto multipunctata*, Paluma, Mt Spec-Crystal Creek National Park, north Queensland, Australia. Photo: Clifford & Dawn Frith]

prey usually fell within a narrower weight range, often below 50-60 g. The weight of prey and the number of animals taken at higher latitudes are also influenced by the Common Barn-owl's need to maintain a higher body temperature than other high-latitude owls and by its sensitivity to cold weather. While various bat species are widely taken, bats never contribute significantly to the overall diet. In 47 of the 52 studies, rodents comprised at least half of all prey items, and in 33 cases over three-quarters. In individual studies, the number of prey species that were recorded as making up at least 0.5% of the total prey items ranged from two to 25. Most diets, however, were dominated by a few species, and of those species recorded with residual representation, together comprising the last 10-20% of many diets, none accounted for more than a small percentage of the diet.

In Europe and North America, the variety of mammalian prey generally declines with increasing latitude, but with some exceptions: for instance, in central Europe up to 18 species were taken, compared with 5-11 in Britain and Ireland and 10-15 in the Mediterranean region. In general, the more productive an area is, the fewer prey species are consumed. For example, where voles are available, a single species can make up 40-90% of the diet. In Australia, all sample studies showed that a single rodent species accounted for over half of the diet, but three of the four studies were carried out when the rodents were in plague numbers so the possible importance of other species needs further study. In Africa, rodents of up to 25 species usually form 80-90% of prey items, but 5-6 species may make up 80% of prey, compared with 3-4 in Europe and 2-3 in North America. In all except arid regions, shrews are the most important non-rodent species.

Where small mammals are scarce or absent and other prey is abundant, Common Barn-owls have adapted locally to alternative diets. In the Namib Desert in southern Africa lizards may comprise about half of the owl's food and scorpions are also important, while a study at the Karnak Temple, in Egypt, found doves (Columbidae) and sparrows (Passeridae) forming nearly half of the diet. In Mali, some pairs depend almost entirely on frogs and toads; and in coastal Guinea-Bissau the diet is dominated by birds, including weavers (Ploceidae), sunbirds (Nectariniidae), kingfishers (Alcedinidae), waders (Charadriiformes) and swifts (Apodidae). On some of the Cape Verde Islands reptiles, particularly geckos (Gekkonidae), are often taken, along

with a variety of birds including plovers (Charadriidae), godwits (*Limosa*), Ruddy Turnstones (*Arenaria interpres*), Collared Pratincoles (*Glareola pratincola*) and weavers. Also in island groups and on some continental offshore islands where seabirds breed, pairs of Common Barn-owls may move in and raise their young entirely on a diet of petrels and shearwaters (Procellariidae), terns (Sternidae) and other seabirds. This is the case, for example, on offshore islands of California (USA), on Razo in the Cape Verde, and for introduced populations in Hawaii and the Seychelles. Some owls also take advantage of communally roosting passerines such as starlings (Sturnidae), thrushes (Turdidae), weavers and Red-winged Blackbirds (*Agelaius phoeniceus*). Such specialized bird-eaters are probably opportunists, like those Common Barn-owls that take advantage of such phenomena as mass hatchings of winged termites.

Both grass-owls are rodent specialists. In Africa, rodents can represent 76-98% of the diet, ranging in weight from 1.5 g to 120 g. African Grass-owls take larger prey, on average, than do co-occurring Common Barn-owls and Marsh Owls. As well as consuming rodents, grass-owls in Africa feed on shrews, elephant-shrews (Macroscelididae), hedgehogs (Erinaceidae), hares (Leporidae) and bats, while Eastern Grass-owls in Australia take dasyurid marsupials (*Sminthopsis*, *Planigale*); both species have also been recorded preying on ground birds, reptiles, frogs and large insects. Inland Australian birds join other owls to take advantage of cyclical rodent plagues. However, several studies have shown that, when prey numbers crash, many grass-owls are unable to find other food and consequently starve.

Greater Sooty-owls are mainly specialists on arboreal mammals such as possums, pygmy-possums and gliders (Burramyidae, Petauridae), but also take terrestrial mammals, including potoroos (*Potorous*), dasyurid marsupials (*Antechinus*, *Sminthopsis*), small wallabies (Macropodidae), forest bats, rabbits and rodents, covering a weight range of 18-900 g. Birds and large insects have also been recorded as prey. In New Guinea, it is likely that large wallabies are consumed as carrion. The Lesser Sooty-owl is more dependent on terrestrial prey, as is the Australian Masked-owl, though its diet is otherwise similar to that of the sooty-owls.

The Oriental Bay-owl is known to eat small mammals. There is little information on the species concerned, but there is an old record of one found dead with the wing bone of a bat protruding

If an intruder, human or otherwise, does not retreat in response to the threat display of a barn-owl, the latter continues with more aggressive behaviour.

It lowers its head and the whole of its upper body and sways them from side to side, while shifting from one foot to the other, with plumage ruffled up to increase its apparent size even more; the wings are lowered somewhat, and the tail spread. Following this, the irate bird shakes its head and moves it up and down, staring straight at the source of danger, all the time uttering loud hissing sounds and from time to time suddenly lunging at the intruder.

If this does not have the desired effect, or if the intruder comes closer, the owl may even make a direct attack by leaning backwards and striking with its sharp talons; occasionally, it may squirt faeces at the enemy. Recently fledged young commonly give such threat displays, and instinctively direct them against mammalian predators, not always unsuccessfully. Tytonid owls do not normally, however, use them against conspecifics. It is interesting to note also that a barn-owl, if picked up by a human being, will not usually put up a struggle; rather, it is likely to lie on its back, with eyes shut, and pretend to be dead. A further point of interest is that, although some owls of the family Strigidae demonstrate certain similarities in threat displays, only the tytonid owls are known to perform the bowing and head-shaking behaviour.



[*Tyto alba pratincola*,
California, USA.

Photos: Tony Martin/
Oxford Scientific Films]



Compared with "typical" barn-owls and grass-owls, the masked-owls and sooty-owls appear to exhibit stronger territoriality. Studies of the Australian Masked-owl, which usually inhabits tall open forest with big trees, have revealed that it exploits all suitable habitat within its range, with the optimal number of pairs maintaining territories; these are estimated to be c. 1000-2000 ha in size. This maximum use of available habitat is paralleled by the Common Barn-owl (*Tyto alba*) in the northern hemisphere, where field research has revealed similar results.

[*Tyto novaehollandiae*, east Australia.
Photo: Eric & David Hosking/FLPA]

from its stomach. Birds, lizards, snakes, frogs and large insects have also been recorded, but it is not known whether mammals form the majority of this owl's diet, nor whether there are regional variations, although among avian prey a preference for flowerpeckers (*Dicaeum*) has been noted in parts of Borneo. Nothing whatsoever is known of the diet of the Congo Bay-owl.

Common Barn-owls hunt in two different ways: by dropping down onto prey from a perch, and by a searching flight low over the ground with occasional hovering and undulations. Their soft, sound-damping plumage, their asymmetrical ears and their heart-shaped facial disc collecting and channelling sound waves, combined with their long legs, demonstrate superb adaptations for nocturnal hunting (see Morphological Aspects). Experiments have shown that Common Barn-owls can hunt efficiently in what is, to a human being, total darkness. Upon locating prey by either sight or sound, they dive in its direction from a height of about 3 m, with talons extended. The long, broad wings provide a low wing-loading that enables slow aerial searching and the carrying of a heavy prey load. Depending on habitat type and diversity, perch-hunting can also be common. In high latitudes such as in northern Europe and North America, Common Barn-owls sometimes hunt in daylight, especially in mid-summer, when there may be little choice, or when rain has restricted nocturnal hunting. Daylight hunting has also been observed in the tropics and may occur widely, provided that it does not lead to mobbing by smaller birds. Common Barn-owls usually hunt alone in a territory, although where prey is particularly abundant, as in Australia during rodent plagues, large numbers may gather in a small area with other owls, including grass- and masked-owls.

Grass-owls hunt by low, quartering flights, gliding and hovering rather like harriers (*Circus*), and usually start earlier and finish later than do the typical barn-owls. Australian Masked-owls, like Common Barn-owls, combine low hunting flights and perch-hunting.

Greater Sooty-owls normally hunt inside closed forest, in the canopy, on tree trunks and on the forest floor. In Australia, they are less inclined to hunt from low perches if there are breaks in the ground cover; in New Guinea, birds inhabiting montane forest also hunt over alpine and subalpine grassland, particularly where there are rocks and other potential cover for prey. Greater Sooty-owls have also been observed to hunt in pairs, with the

male in the canopy and the female close behind but nearer to the forest floor. The Lesser Sooty-owl is also an efficient forest hunter but it makes greater use of low perches, often perching on the sides of tree trunks, and using tracks and clearings. Both sooty-owls are known to hunt at times in total darkness, and the Lesser also forages during heavy rainfall. Although sensitive to habitat disturbance, Greater Sooty-owls sometimes hunt in logged and open areas, even at roadsides, and they take a higher proportion of terrestrial prey, but only where their hunting territory also includes undisturbed forest.

Bay-owls, like sooty-owls, hunt in the forest canopy, and their shorter, more rounded wings are well adapted for rapid flight among the maze of trunks and branches. They also hunt from perches, using the sides of tree trunks, where they rhythmically rock the head, presumably to focus on the location of the prey



Most owl species, when located at their daytime roost or if active before other birds have retired to their nocturnal roost, attract furious mobbing from other birds. Even avian species which do not figure in the owl's diet react in this way, as shown here by these two Black-backed Magpies (*Gymnorhina tibicen*). Perhaps the latter, which feed on smaller birds and mice, regard the owl as a food competitor; but that can be only part of the explanation.

[*Tyto alba delicatula*, Kakadu National Park, Northern Territory, Australia.
Photo: Roland Seitre/Bios]

The members of the Tytonidae are essentially nocturnal. Even though individuals of some species, such as the Common Barn-owl, can sometimes be seen during other hours of the day, the vast majority of the family are unlikely to be visible to the human observer until darkness arrives. Only then does the owl emerge from its roost, as a ghostly aerial figure floating off to its hunting grounds. Tytonids spend the day out of sight in a dark cavity, either in a tree or in dense foliage, or in a suitable niche in a building.

[*Tyto alba alba*,
Toledo, Spain.

Photo: Francisco Márquez]



before rapidly catching it in flight. Again, like sooty-owls, they are strictly nocturnal and it is probable that they regularly hunt in total darkness.

Breeding

The first breeding studies on the Common Barn-owl date back over a century, with observations at the nest going back even farther, to Gilbert White's accurate and highly detailed remarks, in his classic work on natural history first published in 1789, on the behaviour of a pair breeding in his own church at Selborne, in Hampshire, England. In more recent times, several books and hundreds of papers have been devoted to this species, making it the best-known owl in the world. Much of this work is based on the European and North American races, but this is complemented by contributions from Africa, South-east Asia, Australia and South America. However, while details on most of the 28 races of the Common Barn-owl are incomplete, anecdotal or non-existent, a comprehensive picture has emerged that appears generally to characterize the whole genus *Tyto*. For the other *Tyto* species, recent studies have provided a general picture of the grass-owls, the Australian Masked-owl and both sooty-owls, but too little is currently known of the rest of the genus to allow any meaningful discussion of their breeding behaviour. The bay-owls remain poorly known in general, with very limited information available for the Eastern and nothing at all known about the African.

Within the family, then, there is a vast abyss between the state of our knowledge concerning the best-known and least-known species, and for many of our generalizations about the family as a whole we must rely on extrapolating, with caution, from the extensive research carried out on the well-known species. While nothing at all is known of the breeding of six of the species, and next to nothing about two more, the Common Barn-owl continues to be the object of much research, from which very interesting conclusions are emerging. For example, this species featured as the subject of three books in 1994 alone, all based on studies in Britain. One of these, by I. R. Taylor, discusses the results of a 14-year study by the author in Scotland and presents a comparative review of Common Barn-owl studies elsewhere

(see Food and Feeding). In North America, the current research of C. Marti is notable. His 1997 report on the lifetime reproductive success of a Common Barn-owl population in Utah, near the northern limit of its breeding range, is based on data collected from 1977 to 1995. Marti has demonstrated that the owl has a reproductive strategy which is quite unlike that of most other raptors and more like that of a small passerine: a short but highly productive breeding season.

These "passerine" breeding habits associated with the Common Barn-owl may apply to grass-owls too, particularly the inland Australian population. However, from what is known of masked-owls and sooty-owls, their breeding rates are low and are probably influenced by territorial behaviour and habitat availability. Australian Masked-owls are strongly territorial and pair-members may stay together all year, often using the same nest-site over many years. Pairs can be found breeding 1-10 km apart, and in south-east Australia territory size has been estimated at about 1000-1200 ha. Similarly, Greater Sooty-owls appear to mate for life and are also strongly territorial, with territory sizes estimated at about 200-800 ha. They produce a single meagre clutch per season, and may not nest at all in unfavourable years. The spatial distribution of territories in undisturbed habitats suggests that the populations of sooty- and masked-owls have long existed at optimum levels, and that, where there is disturbance, numbers decline because the recruitment rate of young birds is too low. Nevertheless, it has been found that in captivity, with a plentiful food supply, the Greater Sooty-owl will breed when one year old and will raise two broods in a year, each with up to three young, which is about triple the normal breeding rate in the wild.

With their cosmopolitan distribution, Common Barn-owls are always breeding somewhere in the world. Although breeding can start in any month in the tropics, there is some seasonality, with egg-laying usually starting late in the dry season, or in the wetter periods in more arid regions. As latitude increases, distinct non-breeding periods emerge. In northern temperate regions, the source of most data, laying begins with increasing temperatures in spring and coincides locally with the initial breeding activity of mammalian prey species; but the numerous young of such prey species may not be available for another 2-3 months, by which time the owl nests will have half-grown chicks, so warmer weather and the resulting increased activity of small mammals are vital to



Broadly speaking, the principal food of tytonid owls is small to medium-sized mammals. A recent analysis of the diet of the Common Barn-owl, by far the best-studied species, found that small mammals constituted 74-100% of this species' prey in terms of numbers. The analysis examined the results of 52 studies of pellet contents carried out in all parts of the range, thus indicating a very widespread dietary preference. Interpretation of such results requires some caution, however, since not all prey types show up in pellet analyses. Nevertheless, it seems reasonably certain that small mammals are, indeed, the primary food of this species. In rural habitats, the Common Barn-owl is able to exploit a readily available source of rodents: this individual is about to seize a mouse (*Apodemus*) attracted to a sack of grain in an old outbuilding.

[*Tyto alba alba*,
Rackheath,
Norfolk, England.
Photo: P. N. Raven/
Planet Earth]

the actual initiation of a breeding attempt. As a consequence, first laying dates vary widely, depending on annual weather patterns and prey population cycles: ranges of 47 days have been recorded over 12 years in Scotland, and 53 days over eight years in France, but only 15 days over five years in New Jersey, USA. Other influences include habitat variation and the age of females, with older females laying earlier on average. By starting early, a pair may be able to rear two broods, with an average-sized brood taking nearly four months to produce.

The breeding period is usually March-June in northern forms of this species, but if two clutches are involved, the respective periods are usually March-May and June-August. The number of second clutches laid shows much regional variation, and can be linked to the available habitat diversity and the population cycles of small mammals. The laying of three clutches, although rare, has been recorded in a German study and may be more frequent in the tropics, for example in Malaysia. In an extreme case, four clutches were produced within 11 months by a breeding pair in Zimbabwe during a mouse plague. Where the owls depend on more stable and homogeneous agricultural landscapes, the breeding seasons are similar each year. In Australia Common Barn-owl breeding is more opportunistic, with large-scale movements and irregular nesting influenced by temporary increases in local populations of small mammals, but breeding peaks are recorded in March-June and August-November.

Most of the other species for which details are known would seem, like the Common Barn-owl, to have some populations breeding somewhere more or less at all times of the year, mainly due to local variations. This is the case of the African Grass-owl, which breeds when grass cover is at its peak, and thus can be found breeding somewhere within its tropical African range during most of the year; in South Africa, the period is October to July, centred around the austral summer. A similar pattern of local variations emerges for the Eastern Grass-owl, which breeds mainly from October to March in Asia, in May and June in New Guinea, between February and September in coastal Australia, and whenever conditions are favourable in inland Australia. The other three relatively well-known species, those occurring in Australia, can likewise be found breeding at almost any time of year, though they show moderate variations in their peaks: most Australian Masked-owls lay from March to July, northern birds starting earlier; Greater Sooty-owls usually lay between January and September, with a peak around April; while in the Lesser Sooty-owl most egg records are in March-May, the season depending essentially on rainfall. The few records available for the Oriental Bay-owl show breeding from March to May in India, a record of nestlings in November in Sri Lanka, and laying from October to December in Borneo.

Two main kinds of nest-site prevail throughout the family, those situated on the ground amidst grass and those in natural

cavities, typically in trees. The African Grass-owl's nest consists of a flattened pad of grass at the end of a tunnel in a dense grass tuft, often near or under a bush. The nest is part of a network of tunnels which the owls make by pushing through the grass, and these can serve as escape tunnels if the nest is threatened at some stage. The closely related Eastern Grass-owl has similar grass nests with tunnels, though it shows some apparent differences in potential nest-sites, sometimes nesting near mangroves and in young pine plantations.

The sooty-owls, masked-owls and typical barn-owls, as well as the Oriental Bay-owl, are cavity nesters. The Greater Sooty-owl nests mainly in tree cavities, using large tree hollows at heights of some 10-50 m, but it will also breed in rock crevices and caves, preferring large caves with nest-holes high above the floor. There is no nest as such, and the eggs are laid in the debris of the nest-site. The Lesser Sooty-owl likewise nests in tree cavities, and indeed appears to be very similar to the Greater in all aspects of its breeding biology. Australian Masked-owls nest in tree cavities, using large hollows in both trunks and branches, at heights of about 12-25 m, preferring tall trees isolated by location or by their height above surrounding trees. At the chosen site, a depression may be made in the nest debris. Interestingly, in the Nullarbor Plain of southern Australia, in the absence of tree sites, a small population of Australian Masked-owls has adapted to nesting on cliff ledges and in cave clefts. Sadly, though, this population is declining and indeed it may already have disappeared, so the ability of the species to adapt to such sites in the long term remains poorly known. Nothing is known of the other masked-owls, but a Minahassa Masked-owl was recently seen at a probable nest in a tree hole too, and it seems likely that all members of this closely related group will have similar habits. The Oriental Bay-owl's nest is an unlined hollow in a tree trunk or rotten stump, no more than 2-5 m above the ground. One nest-site of this species was recorded as having been used over many years, becoming heavily littered with pellets and other debris. However, a more remarkable case is known for the Greater Sooty-owl, in which birds are often extremely site-faithful; it was calculated that one cave site, according to the layers of prey remains on the floor, had been occupied by countless generations of these owls for about 10,000 years!

A natural cavity-nester, the Common Barn-owl has also become dependent on man-made structures in many parts of its wide range. So long as it has enough room, adequate entrances and exits and little or no disturbance, just about any such structure will be used. Familiar examples include churches, towers, barns, castles, abandoned cottages and warehouses, but nests have also been found in such places as chimneys, wells, duckblinds (hides), unused boats and cavities around bridges. Natural sites are holes in tree trunks, stumps or large, hollow branches, 2-20 m above ground, the tops and hollows of palm trees, cracks and fissures in cliffs, burrows in banks, rock crevices, caves and lava tubes, and even on the ground. Common Barn-owls readily take to nestboxes, usually provided as part of local conservation plans, but also used in some areas to effect rat-control programmes, such as in oil palm plantations in Malaysia. Preference for natural sites varies regionally, and is more widespread in the USA than in Europe. While all populations of this species are sensitive to the presence of human activity, North American birds appear to be more so than their European counterparts, although this may be partly a consequence of the presence of more mammalian nest-predators such as raccoons (*Procyon*).

Nest construction in the Common Barn-owl involves making a slight scrape or depression, where possible, and the female using pellets and other debris to form a pad for the eggs, with an insulating layer of mammal hair from the pellets. In the south-western USA, the owls wholly or partially excavate a nest-burrow up to about 1 m deep in a bank or cliff. Some pairs make use of large abandoned nests, such as those of Ospreys (*Pandion haliaetus*), or take over, or more rarely share, active nest-sites of other birds, such as Eurasian Jackdaws (*Corvus monedula*). In this owl species, too, sites may be occupied for several seasons.

In the Common Barn-owl, breeding activity usually begins 6-8 weeks before laying, but there is much individual variation, particularly in the behaviour of males. Some roost with the female at the nest-site during winter, although most roost apart. Males start spending more time at potential nest-sites at night and call more frequently, presumably to advertise ownership of the site and to attract a mate. They also use a ritualized advertising display flight, call in flight, and make short aerial excursions over the area around the nest-site with stiffened, deliberate

Once caught, prey is carried back to the nest, or to a favoured feeding spot, in the bill. This is one of the ways in which the feeding and foraging habits of both families of the order Strigiformes differ from those of the diurnal birds of prey (Falconiformes), which normally carry food in their talons. Direct observation and photographic evidence help to confirm the results of pellet analysis in determining the diet of owls: it is quite remarkable how frequently tytonids are shown to be carrying or about to swallow rodents.

[*Tyto alba alba*,
near Reims,
north-east France.

Photo: Gerard Lacz/NHPA]



wingbeats. The time the male spends in and around the nest peaks in the two weeks before laying and during laying, but when the clutch is complete most males return to their usual roost-site. This form of mate-guarding also involves frequent copulation, starting before hunting begins and being repeated many times during the night. Much of the courtship behaviour of the Australian Masked-owl is apparently similar, males calling from nest-sites for potential mates; in display flight the male circles around high above the tree tops, calling the whole time.

An important part of courtship behaviour in the Common Barn-owl is food presentation, not only to maintain the pair-bond, but also to facilitate the necessary weight increase of the female for egg production, which can influence the size and timing of the clutch. The female stays at the nest for 10 days prior to laying, when the male provides all the food, often in excess of her requirements. Unmated males may accumulate large stockpiles of prey in their efforts to attract a mate. In this pre-laying period sexual chases occur, in which the male and female fly in and around the nest-site at high speed. Inside the cavity, they indulge in a great deal of bill-fencing, mutual preening, tongue-clicking, squeaking, twittering and hissing. In a few cases where a male attracts more than one female to the nest, he may mate with the second female; the latter then produces a clutch at a nearby nest-site, but is usually less productive. Taylor found seven such cases in 14 years of study.

The eggs tend to be a rounded ovoid, though those of the Eastern Grass-owl are more pearl-shaped. It is highly typical of both *Tyto* and *Phodilus* that the eggs are white when laid but soon become discoloured by nest debris. In rare instances, at least in the Common Barn-owl, newly laid eggs may be marked with brown flecks. Average weights of fresh Common Barn-owl eggs are 17.9 g for the subspecies *alba*, 17.5 g for *guttata* and 26.6 g for *pratincola*, the first two representing 4.9% of the female's weight and the third 4.8%. The small egg size in relation to the female is characteristic of cavity-nesting birds, but in this species it seems also to be an adaptation to large clutch size, and an aid to raising large broods.

Clutch size is rather variable across the family, with sooty-owls and masked-owls laying much smaller clutches than those of the typical barn-owls and grass-owls, and bay-owls perhaps in an intermediate position. The data collected to date show: 1-2

eggs, usually two, in the Greater Sooty-owl; 2-4 eggs, usually just two, in the Australian Masked-owl; 3-5 eggs in the Oriental Bay-owl; 2-6 eggs, normally four, in the African Grass-owl; 3-8 eggs in the Eastern Grass-owl; and 2-14 eggs, most commonly 4-7, in the Common Barn-owl. It is noteworthy that in the Common Barn-owl, with its large clutch, most of the hatched chicks survive, whereas from the Greater Sooty-owl's typical clutch of two normally just a single chick survives. The laying interval ranges from two days for the Eastern Grass-owl, to at least 2-3 days for the Common Barn-owl, and about four days for the Greater Sooty-owl.

Intraspecific variation in clutch size is, of course, best known in the Common Barn-owl. In Scotland, Taylor found that earlier clutches were larger, but the opposite was the case in studies he compared from Germany, France and Mali. The variations appear to be influenced by changes in vegetation cover, prey numbers and prey activity, and, in Scotland, by the better survival of young fledged from earlier clutches, regardless of clutch size. However, in years of peak prey abundance, 15% or fewer of the Scottish pairs laid a second clutch, whereas those in central Europe and Mali had a higher incidence of second clutches. In years of low food supply some pairs do not breed, but the extent to which this occurs is unknown.

In the Common Barn-owl, and probably in other species, the female effectively undertakes all the incubation, and she develops a brood patch for this purpose, a feature absent in the males, which rarely sit on eggs and then only for brief periods. In the Common Barn-owl, incubation lasts 29-34 days, usually 30-32 days, which is about 10% longer than for other cavity-nesting owls. However, the period is even longer in most other hole-nesting tytonids, taking 35-42 days in the Australian Masked-owl and about 40-42 days in the Lesser Sooty-owl. It can be equally lengthy in the ground-nesting grass-owls, taking 32-42 days in the African, though about 31 days in the Eastern.

A few days before hatching, young Common Barn-owls can be heard calling from within the egg. Most of them hatch overnight, using the egg-tooth, and the female sometimes assists by removing pieces of shell and fragments of membrane. Broken shells and unhatched eggs are typically left in the nest. The hatching success rate in this species is related to egg quality and food supply but does not seem to vary greatly. Examples of 83% in

One of the two ways in which Common Barn-owls hunt is by slow searching flight low over the ground, occasionally hovering briefly, or from time to time rising or falling a little. This slow quartering is made possible by the long, broad wings, which provide low wing-loading. Such foraging usually takes place over areas of long grass or similar rank vegetation, or along edges of ditches or dykes. On locating prey, either by sight or by sound, the owl dives on to it. Although this species not uncommonly forages in the half-light just before or just after night, it is able to hunt with equal success in total darkness.

[*Tyto alba alba*, Norfolk, England. Photo: Richard Brooks/Aquila]



Mali, 82% in France, 71% in Germany and 69% in Malaysia were quoted by Taylor, who recorded rates of 85% in plantations and 76% in farmland. The majority of eggs that failed to hatch were found to be the last or penultimate eggs in their clutches, and the few complete hatching failures involved females which were underweight as a result of food shortages.

When hatched, European Common Barn-owl chicks weigh about 13-14 g. Hatching is asynchronous, at intervals usually of 2-3 days, producing a size hierarchy. African Grass-owl chicks hatch within 1-2 days of each other, and the evidence suggests that size differences are probably, correspondingly, slightly less marked. At a Sri Lankan nest of the Oriental Bay-owl, the three nestlings found were of different sizes, indicating that *Phodilus* also exhibits the asynchronous hatching characteristic of *Tyto* species.

In the Common Barn-owl, the first down, the neoptile, is sparse and the chicks need to be brooded by the female until the second, mesoptile, down starts to grow after 12 days, this becoming fully developed by about day 20. They are not left alone in the nest until the youngest is 12-16 days old, and they huddle together to minimize heat loss. The growth rate of chicks peaks at 16-19 days, with an increase of 12-14 g per day recorded in Europe and 22 g per day in the USA. Weight gains vary, depending on whether the broods hatched earlier or later in the breeding season. Young Common Barn-owls reach their maximum weight by 36-40 days, when they weigh more than their parents; depending on food supply and the number of young in the brood, they may stay above the adult weight when they leave the nest. Skeletal growth is also completed by about day 40. Growth of primary feathers starts around day 10, but these are not fully developed until the young are 70-75 days old.

Prey-delivery rates to 19 Common Barn-owl nests studied in Scotland were obtained by using automatic recording equipment. Rates increased from around 8-10 times per 24 hours during incubation, when the female was fed on the nest, to a peak of 14-16 times when the chicks were about 30 days old, an average of 4.2 items per chick per day; they declined thereafter, but with some prey still being delivered when the youngest chick was about 85 days old. The estimated daily food intake per chick during the peak consumption period at 30-40 days was 98-108 g.

Such details are essentially lacking for the other members of the family. However, it is worth noting that the total fledging

period shows considerable variation, ranging from about 42 days in the African Grass-owl, and some 60 days in the Eastern Grass-owl and the Greater Sooty-owl, to about 70-84 days in the Australian Masked-owl, and 90 days in the Lesser Sooty-owl; the period is unknown for both bay-owl species. In many species the fledged young are known to take some time before becoming wholly independent, and while both grass-owl species and the Australian Masked-owl will stay near their nests for several weeks, the young Greater Sooty-owl remains with its parents for up to six months.

Variations in the mortality rates of Common Barn-owl chicks are linked to food supply and usually affect the younger members of the brood. For example, in Scotland, when prey numbers were low, the mortality rate was 26% for first-hatched young and 94% for the last. The overall mortality rate between hatching and fledging was 5-10% in years of high prey abundance and about 45% in low years. In high-abundance years, 70% of deaths were of chicks under 10 days old, and very few died after day 20. In poor years, most died before day 20 but numbers of deaths up to fledging were substantial. Dead chicks in nests are usually fed to their siblings.

Regionally, annually and within breeding seasons, there is much variation in the fledging success of Common Barn-owls. All variations can be attributed to food supply, but habitat differences may also be influential. Long-term studies have shown total production of young per pair per year to range from 1.6 in the Galapagos Islands to 7.0 in Malaysia, with a range of 3.1-5.3 in Europe and 1.9-4.0 in the USA. A German study examined annual changes in the number of fledged young per pair over seven years and three cycles of peak prey numbers; the results were 2.4-4.3 for first broods only, and 2.4-7.1 for first and second broods combined, where second broods were produced in five of the seven years by 17.1-55.6% of females.

In his study of the lifetime reproductive success of a Common Barn-owl population in Utah, USA, from 1977 to 1995, C. Marti found that it varied widely among individuals, with a few birds producing a disproportionate number of the next generation. Compared with other raptors, including four other species of owl, on which similar studies have been undertaken, the Common Barn-owl has moved in the direction of trading ■ long life for rapid and intensive reproduction. The early maturation, large

Prey items, when not carried back to the nest or deposited nearby for later consumption, are normally taken to a perch to be eaten. If not too large, prey are swallowed whole; bigger items are pulled apart before being eaten piecemeal. In certain circumstances, such as during rodent plagues, larger numbers of owls of several species, along with other predators, may assemble in one area to take advantage of the easy pickings. In most cases, however, tytonids hunt solitarily within their own foraging territory.

[*Tyto alba alba*,
Buckinghamshire,
England.

Photo: Andy Rouse/DRK]





clutch size, multiple clutches and low survival rate are characteristic of species adapted to harsh environments. Common Barn-owls must reproduce quickly and intensively to maximize their fitness. Marti studied 357 nesting attempts by a minimum of 473 birds and documented the history of 262 individuals. On average, the age of first breeding was 1.06 years, the number of years of breeding was 1.30, and the number of years of breeding successfully was 1.03. In one year, 11% of the pairs produced two broods. The average number of eggs produced in a lifetime was 9.76, and of young fledged 5.58. Of the females that laid eggs, 8% laid a quarter of the population's eggs, 55% laid three-quarters and 22% produced no fledglings at all; 12% left breeding descendants, with up to four generations traced, the number of direct descendants ranging from three to 69. The age when females started breeding had no strong effect on lifetime success, and breeding age had a negligible effect on clutch size and the number of fledglings produced in a single season. Other potential influences on lifetime reproductive success examined in this study were habitat variability, age and sex of individuals, and variability of winter severity. The first of these three factors was found to have no influence, while age and sex had very little; harsh winters, however, had a strong negative influence on adult survival and clutch size, but none in terms of numbers of fledglings produced in the next breeding season.

Movements

All tytonid owls are essentially sedentary, even at higher latitudes, although some post-breeding dispersal does occur, especially among first-year birds. Breeding pairs normally stay within their territories, but, depending on food supply during non-breeding periods, they sometimes wander into the territories of other pairs; the extent of such movements may also be influenced by territory size and adult mortality rates. Fidelity to both nest-site and mate, which were found to be over 90% for Common Barn-owls in Scotland over two consecutive years, also support the idea of generally sedentary breeders, but it is not yet clear how far these results can be applied elsewhere. For example, a high

fidelity rate seems to be shared by Common Barn-owls in France and west-central USA (Utah), but not by those in Germany and eastern USA (New Jersey).

Known dispersal of tropical forms includes records from offshore islands and other areas outside the habitats normally frequented, such as would result from altitudinal movements. Such observations are few, however, and the evidence suggests that the normal pattern is for adults to stay in or close to their breeding territories, with most records from elsewhere attributable to post-breeding dispersal of first-year birds. The extent of dispersal in the tropics and subtropics is unclear but it is probably not great, although the recovery at Bo, in southern Sierra Leone, of a Common Barn-owl 1000 km from where it had been ringed at St Louis, northern Senegal, is notable, as also is an observation of an African Grass-owl from Ethiopia, some 900 km outside its normal known range. An exception to the general pattern appears to be in Australia, where some populations of Common Barn-owls and Eastern Grass-owls, particularly those occurring inland, are highly nomadic. These owls undertake irruptive movements associated with rodent plagues, as well as seasonal dispersal north and east in winter, and some movement away from coastal areas in summer. Ringing recoveries of Common Barn-owls involving distances of 65-840 km have been reported from south-east Australia, with vagrants reaching as far as New Zealand.

Inland Australian grass-owls generally disperse to northern coastal regions, where they also breed. Evidence suggests that northern coastal-breeding birds are not resident all year round. This temporary northward dispersal may also account for grass-owl records farther north, from some Indonesian islands and southern New Guinea. North of the equator, too, there is some evidence of dispersal, with possible vagrants in Hong Kong, involving the race *chinensis*, and one record from the southern Ryukyu Islands, the latter a bird of the Taiwanese race *pithecopus* or possibly the Philippine race *amauronota*. Vagrants have occurred in New Caledonia, Fiji and south-west Australia, but dispersal to south-east Australia may include temporary breeding activities. The wide but scattered occurrence of the Australian Masked-owl in parts of central and southern Australia is also a consequence of nomadic behaviour in some regions. All records of long-distance movements of sooty-owls, however, probably involve first-year birds only.

Most information on dispersal patterns comes, inevitably, from studies of post-fledging dispersal of European and North American Common Barn-owls, based on direct observations, ringing recoveries and radio-tagging. There is much regional variation, but in general most British birds disperse to within 20 km, European birds to within 50-100 km, and North American birds to beyond 80 km in the north and within 80 km in the south. Both continents have recorded long-distance recoveries, up to 1600 km in Europe and 1760 km in North America. Young ringed in the Netherlands, for example, have been recovered about 1500 km away in Spain and Ukraine. The evidence suggests that such movements are not entirely the result of severe winter weather. While birds may disperse in all directions, most move southwards. Barriers to dispersal include mountains and large water bodies, yet there are vagrancy records that obviously required over-water flights, one example being the recovery in Bermuda of a bird ringed about 1250 km away in New Jersey. However, Common Barn-owls have been found on ships up to 360 km from land and on offshore oil rigs; such assistance may account for some of the long-distance records, a circumstance not confined to owls. The most unusual evidence of assisted long-distance vagrancy comes from several of the New Zealand records of Common Barn-owls which were of birds travelling in the undercarriage bays of large aircraft. One of these apparently arrived from North America and, not surprisingly, was found dead on arrival, but Australian birds have survived the rigours of the flight and some of the survivors are even suspected to have been "stowaways" from Fiji.

From ringing recoveries in Britain, it has been found that within the first 1-2 weeks after fledging 37% of Common Barn-owls had dispersed over 3 km from the nest, the figure increasing to 59% by 5-6 weeks. Radio-tagging of eight individuals in Wales revealed that movement away from their respective nests varied, with two

Although rodents and other small mammals form the basic diet of the Common Barn-owl, its food spectrum ranges from larger mammals, birds, reptiles and amphibians to fish, insects, spiders and scorpions, and earthworms. A surprisingly wide variety of birds has been recorded as prey of this owl. Passerines, such as this Blackbird (*Turdus merula*) are among the most frequently taken, but in some parts of its range this owl actually specializes on seabirds, such as shearwaters and petrels (*Procellariidae*) and terns (*Sternidae*); in other areas, waders (*Scolopacidae*) and plovers (*Charadriidae*) can make up a significant proportion of its diet.

[*Tyto alba alba*,
Buckinghamshire,
England.
Photo: Andy Rouse/DRK]



The sooty-owls of Australia and New Guinea hunt mostly in closed forest, where they feed on both arboreal and terrestrial mammals, supplemented by far smaller numbers of birds and insects. Common prey animals include dasyurid marsupials, and pygmy-possums and gliders (Burramyidae, Petauridae). Both species are known to be capable of hunting with great efficiency in total darkness, and this is reflected in the size of their eyes, which are larger than those of any other tytonid.

The Lesser Sooty-owl will also hunt during heavy rainfall. The latter species catches some of its prey in the forest canopy, but, compared with the Greater Sooty-owl (*Tyto tenebricosa*), it tends to make far more use of the middle and lower forest strata, often using low perches and the sides of tree trunks, and sometimes exploiting the opportunities offered by clearings and forest tracks.

As a consequence, it catches a greater percentage of terrestrial prey than does its somewhat larger relative, a fairly large proportion of its diet consisting of ground-dwelling rodents.

The Lesser Sooty-owl depicted here would appear, from its rather heavily patterned underparts, to be a subadult. Having caught a rodent, it proceeds to swallow it whole in the manner typical of the family.

[*Tyto multipunctata*,
Jilatten,
north-east Queensland,
Australia.
Photos: Marco Sacchi]



A high frequency of copulation is characteristic of the Common Barn-owl. The peak in this activity generally occurs in the two weeks prior to egg-laying and continues during the laying period; at this time in the breeding cycle, matings can be repeated almost without a break during the night. The rate of copulation decreases during the incubation and chick-rearing periods, but does not cease altogether. The pair shown here had young four weeks of age, yet continued to mate. Such behaviour serves to reinforce what is already a very strong pair-bond.

[*Tyto alba alba*, near Ringwood, Hampshire, England. Photo: Mike Read/Planet Earth]

birds leaving at each of 2-3, 3-4, 4-5 and 6-8 weeks after fledging. This variation may relate to such factors as the extent of parental post-fledging feeding, availability of prey, competition from other owls, and the learning of hunting skills. In Germany, 27% of ring-ing recoveries within a month of fledging were at over 10 km and 18% were between 50 km and 100 km; in the second month, 27% were found less than 10 km away and nearly 40% more than 50 km away, with dispersal stabilizing 4-5 months after fledging.

Studies of overall movements indicate that in Britain 53% of birds bred within 10 km of their natal site and 90% within 50 km; in Denmark 86% bred within 50 km; in Germany fewer than 40% nested within 50 km and 30% at over 100 km; and in France and the Netherlands 70% bred within 50 km. More evidence is required, but it appears that most females disperse farther than most males; in Scotland, for example, males usually settle within 5 km of their natal site, but females usually at 6-10



Among tytonids, and indeed all members of the Strigiformes, the task of incubating the eggs is undertaken by the female. The male's responsibility is to supply food to his mate. On rather infrequent occasions, however, the male will cover the eggs for a short period if the female leaves the nest; unlike the female, however, he does not possess a brood patch, and would consequently be far less efficient were he to attempt incubation proper. Such egg-covering by the male is always brief, and he immediately stops when the female returns.

[*Tyto alba alba*, near Ringwood, Hampshire, England. Photo: Mike Read/Planet Earth]

Favoured nest-sites are often used repeatedly over a considerable period of time. This tree hollow, situated in a dense rainforest, had apparently been used by Lesser Sooty-owls for many years in succession. The floor of the cavity is littered with numerous skulls of mammals, and some bird skulls. The female is about to consume a pygmy-possum (Burramyidae), a common prey of this species.

[*Tyto multipunctata*, near Ingham, north Queensland, Australia.
Photo: John Young]



km. This dispersal pattern may help avoid inbreeding, but the relatively small distances involved still indicate a high proportion of closely related individuals in local populations. The wider movements of mainland continental birds suggest a more successful strategy for maintaining genetic diversity. While inbreeding is a potential problem in all island or otherwise isolated populations, it would be of interest to compare the situation in Britain with that of Common Barn-owl populations living on much smaller islands.

In North America, northern and southern (up to 3° N) populations of Common Barn-owls show marked differences in post-fledging dispersal. In 1952, P. A. Stewart reported that 56.8% of ringing recoveries of northern birds were within 80 km of their natal sites, with 31% more than 160 km away, but for southern birds 88% were within 80 km and none was found more than 160 km away. Basing his conclusion on mostly southern recoveries of northern birds over six months old, 43.7% of which were found over 160 km and 27.7% over 320 km from their natal site, and on other evidence, Stewart considered northern birds to be partly migratory. This has been discussed by later authors based on observations at Cape May, in New Jersey, where large numbers of owls have been recorded in autumn. In his recent book on Common Barn-owls, I. Taylor attributed such movements to post-fledging dispersal, in no specific direction, where large numbers indicated a good breeding season in nearby areas of good habitat. As in Europe, such movements, including long-distance vagrancy, may be the consequence of periods of low prey abundance.

In tropical island groups, such as Fiji, inter-island movements of Common Barn-owls are frequent. In Indonesia, there has been a westward movement of this species over the past 30 years from Java north through Sumatra and smaller islands to the Malay Peninsula. This form of range expansion demonstrates the species' well-known adaptability to habitats and nesting sites associated with human activity, and is similar to its northward expansion in temperate regions over longer periods. Elsewhere, island vagrants may stay on and breed, sometimes permanently, as on Bermuda since 1931, and possibly in the Falkland Islands, where breeding was first recorded in 1989. Historically, such events may well have formed the basis of the radiations hypothesized to have occurred in this family (see Systematics).

Relationship with Man

Since ancient times, and across all cultures, owls have fascinated people. Few other birds have accumulated such a wealth of varying and contradictory beliefs about them. Owls may be either feared or venerated, despised or admired, considered lucky or unlucky, and wise or foolish. They are associated with a wide range of superstitions concerning magic and witchcraft, prophecy, weather, birth, death and many other natural and unnatural phenomena. Owls may turn up in potions, medicines and even recipes.

With its widespread occurrence, nocturnal habits, nesting associations with humans, ghostly appearance and shrieking voice, the Common Barn-owl is probably the source of many recurring owl themes in myths and folklore. It is the White or Ghost Owl, the Demon Owl, the Screaming, Screech or Scritch Owl, even the Hissing Owl; in German it is the *Schleiereule*, the Phantom (or Mystery, or Veiled) Owl; and in French *Chouette effraie*, the Owl of Evil Omen. Another name is the Monkey-faced Owl, suggesting something uncannily "human" about the owl's face, helping it to an association with witchcraft not only as a witch's "familiar", but possibly even as a witch in another form. While it is more likely to be associated with death and the worst of owl superstitions, in some areas the Common Barn-owl can be a symbol of good fortune and luck. As to wisdom, this is usually the province of other owls, for example the Tawny Owl (*Strix aluco*) in Europe.

Common Barn-owls are known to have been present in Britain for at least 10,000 years, and their bones were found among the remains of an Iron Age village at Glastonbury. In Ancient Egypt, identifiable Common Barn-owls are known from wall paintings and bas-reliefs, though varying in details of feather work and head decoration over the dynastic periods. This owl is also among at least six species identified from mummified remains in tombs. Some Egyptians believed that a person had three souls, with the third, named *Ba*, represented as a human-headed bird never flying far from a person's burial site. This belief is thought to have derived from the fact that owls were seen frequenting tombs and temple sites. Today, Common Barn-owls may still be found around such ancient sites. The owl symbol, used in hieroglyphic script as the bird itself or the "m" sound, is variably represented and can resemble the Common Barn-owl as depicted in other forms.



Common Barn-owls use a wide range of nest-sites throughout their range. Man-made structures, including barns, are widely exploited, while natural sites are commonly hollows in tree trunks or large branches. The young are reared on a small scrape lined with pellets and other debris, with mammal hair from the pellets also providing some additional insulation. Chicks are brooded by the female continuously for about two weeks, after which both parents leave to hunt. At this latter stage the young, now in their more protective second (mesoptile) down, huddle together for warmth while the adults are away; since hatching is asynchronous, at intervals of 2-3 days, there is a noticeable size difference among the chicks. By c. 16 days of age, the owlets are able to dismember food themselves, or swallow it whole; they grow rapidly, their weight increasing by up to 22 g daily during the peak growth period at around 16-19 days. In the first week or two of their life, however, they are comparatively helpless and are totally dependent on the female for warmth and food; during this period, the female receives prey from her mate and feeds it to the small chicks bill to bill.

[Above: *Tyto alba pratincola*, California, USA.
Photo: S. Maslowski/FLPA.



Below: *Tyto alba alba*, near Ringwood, Hampshire, England.
Photo: Mike Read]

In pre-Columbian America, the owl motif is widespread. While often highly stylized in carvings, totems, masks, fetishes, pottery and other objects, some of these motifs suggest the influence of the Common Barn-owl in particular. For example, a jar from the Mochica people of northern Peru (about 300 BC to AD 800) features an owl with a face mask like that of this species and clutching a rodent in its bill, perhaps indicating an early recognition of this owl's beneficial association. Mayan hieroglyphics, too, include owl symbols, probably representing deities such as

Ah Puch, the god of death, also linked with the god of war and human sacrifice.

This association with death is found among the Zapotec of southern Mexico, who believe that the Common Barn-owl is commissioned to give notice when a man is about to die, and then to go and fetch the soul. In other indigenous New World cultures, owls symbolize courage and strength and sometimes play a symbolic role in warfare, or represent wisdom or animal trickery. These are also recurring themes in other cultures, thus

It is hardly surprising that the Common Barn-owl, with its cosmopolitan distribution, exhibits a very broad range of ecological breeding adaptations. In the USA, the species seems to have a greater preference for natural sites than it does in Europe, and in desertic regions of the former continent it often nests in holes in cliffs or even in the ground.

The dark subspecies inhabiting the Galapagos Islands makes frequent use of cave sites: the individual shown opposite had chosen a small cave in the side of a dry creek bed in the humid highlands, at an elevation of c. 500-600 m.

It is interesting to note that, in the Galapagos, this species fed primarily on the introduced black rats (*Rattus rattus*), following the extinction of the endemic rice-rat.

Common Barn-owl clutches can contain up to 14 eggs, although 4-7 is more usual. Most of those chicks which hatch survive to fledging, although there is a great deal of variation.

Long-term studies have shown the total production of young per pair and per year in the Galapagos to be only 1-6, whereas in Malaysia it is as high as 7-0.

[Above: *Tyto alba pratincola*, Sonoran Desert, Arizona, USA.

Photo: John Cancalosi/Auscape.

Below: *Tyto alba punctatissima*, Santa Cruz, Photo: Tui de Roy]



demonstrating a universal theme in how the appearance and behaviour of owls may be interpreted. For example, among some Aboriginal peoples of Australia, a kinship between each woman and the lives of her mother, sisters and daughters was connected to the lives of certain owls and other nightbirds, such as frogmouths (*Podargus*); all "birds of evil omen" were protected by the women, however, since it was unclear which owl guarded which particular soul. Totemic carvings featuring the Common Barn-owl are known from New Ireland, off north-east New

Guinea, where the owl symbol is associated with honouring ancestors; this is of wider interest, as no barn-owl species is definitely recorded from New Ireland.

In the Bible, owls, along with other predators, were considered unclean and were also associated with destruction and ruin. The association with ruins may well have involved the Common Barn-owl, one of at least eight species identified from biblical texts. This species, frequently referred to as the "Screech Owl", or equivalents, throughout literature, appears in Pliny's *Historia*



Grass-owls, as their name implies, are closely associated with grassland habitats. Unlike other members of the family, they nest only on the ground. The typical nest of the African Grass-owl consists of a flattened pad of grass at the end of a grassy tunnel. The owls push their way through the vegetation to create a network of such tunnels, which the adults and young later use as escape routes should the nest be threatened.

The Eastern Grass-owl (*Tyto longimembris*) has similar nesting habits, although it sometimes selects sites below mangroves or in young pine plantations, whereas its African counterpart almost invariably nests near a bush.

[*Tyto capensis*, Transvaal, South Africa. Photo: John Carlyon/Aquila]

Naturalis as a bird of ill omen and an associate of witches, but with some positive aspects. For example, the feet of a Screech Owl burnt together with the herb plumbago is claimed to be effective against snakes. Pliny also advised that, if one lays the heart of a Screech Owl on the left side of a woman as she lies asleep, she will disclose all the secrets of her heart. In his *Booke of Secretes* (1525), Albertus Magnus offered a different version: "For if the heart and right foot of it be put upon a man sleeping he shall say anon to thee whatsoever thou shalt ask of him."

The influence of Pliny endured for many centuries. By the Middle Ages, owls were firmly established in European minds as fearful creatures associated with evil, death, witchcraft, mischief and the unknown. The owl could also be a guardian against the darkness, a theme represented by Michelangelo in his sculpture *Night*, depicting a Common Barn-owl standing alert at the feet of a naked, sleeping woman. When William Shakespeare needed to emphasize the fears and superstitions of his characters, owls were prominently featured, and such symbolism was well understood by his audience of that time. The Common Barn-owl, again as the Screech Owl, provides a good illustration of this:

"The owl shriek'd at thy birth, an evil sign;
The night-crow cried, aboding luckless time;
Dogs howl'd, and hideous tempest shook down trees!
The raven rook'd her on the chimney's top,
And chattering pies in dismal discord sung."
(*Henry VI, Part III*, V, 6);

"Now the wasted brands do glow,
Whilst the screech owl, screeching loud,
Puts the wretch that lies in woe
In remembrance of a shroud.
Now is the time of night
That the graves, all gaping wide,
Every one lets forth his sprite,

In the church-way paths to glide."
(*A Midsummer Night's Dream*, V, 2);

"It was the owl that shriek'd, the fatal bellman,
Which gives the stern'st good-night...
I heard the owl scream and the crickets cry."
(*Macbeth*, II, 2);

and when the witches of Macbeth add a "howlet's wing" to their boiling cauldron, the Screech Owl would seem to be the best source. Compare Ben Jonson in his *Masque of Queenes*:

"The screech owl's egg and the feathers black,
The blood of the frog and the bone in his back,
I have been getting, and made of his skin
A purset, to keep Sir Cranion in."

As well as being prescribed as potions, parts of owls or their eggs were a feature of various folk remedies. For better eyesight, charred and powdered owls' eggs could work, or one could just eat the eyes, depending on where one lived. The use of owl eggs to relieve drunkenness or to bring about a dislike of wine dates back to classical times. This remedy was updated in 1635 by John Swan, in his *Speculum Mundi*: "The egges of an owl broken and put into the cup of a drunkard, or one disirous to follow drinking, will so work on him that he will suddenly lothe his good liquor and be displeased with drinking."

One French variation was to make an omelette of five, nine or 13 owls' eggs. Salted owl could also work. In Poland, rheumatism could be cured by burning owl feathers over charcoal, or eating baked owl. As with the cure for drunkenness, all such folk remedies seem to have ancient roots. Pliny offered a few in the first century, one of which, said to cure haemorrhage, involved the Common Barn-owl: "The bird known as the screech owl is boiled in oil, ewe milk butter and honey being added to the preparation when properly dissolved."

Apart from any purported medicinal properties, owls have appeared on the menu in various parts of the world, with examples dating back at least to ancient Babylon. While owls continue to be offered as a delicacy in some countries, such as China, this is likely to be connected to the survival of folk remedies requiring owls as part of regional traditions of herbal medicine.

The age-old art of storytelling in the form of fables dates back to ancient Indian and Greek texts, notably of Aesop, and features owls as wise or foolish depending on the moral of the tale. These stories, in prose or verse, like many myths and superstitions concerning owls, do not usually enable identification to species, but some certainly suggest the Common Barn-owl as their inspiration:

An Owl of grave deport and mien,
Who (like the Turk) was seldom seen,
Within a barn had chose his station,
As fit for prey and contemplation.
Upon a beam aloft he sits,
And nods, and seems to think, by fits.
(So have I seen a man of news,
Or Post-boy or Gazette peruse,
Smoke, nod, and talk with voice profound,
And fix the fate of Europe round.)
Sheaves piled on sheaves, hid all the floor:
At dawn of morn to view his store
The Farmer came. The hooting guest,
His self-importance, thus exprest:
"Reason in man is mere pretence:
How weak, how shallow, is his sense!
To treat with scorn the Bird of Night,
Declares his folly or his spite.
Then, too, how partial is his praise!
The lark's, the linnet's chirping lays,
To his ill-judging ears are fine,
And nightingales are all divine:
But the more knowing feather'd race
See wisdom stamp'd upon my face.
Whene'er to visit light I deign,
What flocks of fowl compose my train!
Like slaves they crowd my flight behind,
And own me of superior kind."
The Farmer laugh'd, and thus replied:
"Thou dull important lump of pride!
Dar'st thou with that harsh grating tongue
Depreciate birds of warbling song?
Indulge thy spleen: know, men and fowl
Regard thee, as thou art, an Owl.
Besides, proud Blockhead! Be not vain
Of what thou call'st thy slaves and train:
Few follow Wisdom or her rules;
Fools in derision follow fools."
(*The Owl and The Farmer* from John Gay's *Fables*, 1727)

Since the eighteenth century in particular, the association of Common Barn-owls with farms, as well as their known preference for eating rodents, has made them welcome visitors to farms and gardens in many regions, with some farmers even encouraging them to nest by adapting barns and other buildings. The many superstitions associated with these owls have also played a part in such arrangements, as for example in Brittany, in north-west France, where the sighting of an owl in a field was a sure sign of a good harvest to come. In parts of England, it was thought that a scarcity of owls to control rodents could be resolved by hanging a dead owl on or above the barn door. This same custom was followed elsewhere in England, as well as in Germany and France, as a means of averting bad weather, and in Italy to ward off "the evil eye". Even today, in some regions, owls are still shot, trapped or beaten to death to allay various fears or superstitions.

The reputation of the Common Barn-owl as a rat-catcher has led to several attempts to introduce it on small islands as a means of biological control. Regrettably, all such attempts have failed to control rats and, moreover, have had an adverse effect on indigenous bird populations. Introduced in the Seychelles from

Kenya in 1951 and 1952, the owls became a serious threat to the endemic avifauna and local breeding seabirds such as the White Tern (*Gygis alba*), and a bounty was placed on their heads in the 1960's. Common Barn-owls from California which were introduced in Hawaii in 1958-1963 also affected bird populations, including seabirds on their offshore breeding islets. Following the arrival of rats on Lord Howe Island in 1918, attempts to introduce Common Barn-owls from Australia in 1923 and from California in 1927 were unsuccessful, later records being attributed to vagrancy. Australian Masked-owls, however, introduced on the island from 1922 to 1930, did manage to establish themselves, although they, too, have had an adverse impact on local bird populations, including breeding seabirds. The endangered and endemic Lord Howe Rail (*Gallirallus sylvestris*), known colloquially as the Woodhen, was also affected and, as part of the Woodhen Management Plan, the shooting of these owls was considered the most effective control, with 35 shot in 1988-1990. The owl can, indeed, be a bad omen for the local birdlife.

Centuries of folklore and superstition will take a long time to die out or change. Some may even be reinforced in spite of alternative and more logical explanations. For example, in Britain Common Barn-owls are known occasionally to "glow" in the dark, enhancing the image of the ghostly night hunter. A recent explanation is that, when an owl roosts in a hollow tree where luminous bacteria and fungi occur, particles of these organisms may sometimes adhere to its feathering. Some individuals glow quite brightly, as demonstrated by the observations reported in the *Transactions of the Norfolk and Norwich Naturalists' Society* in 1907:

"There are two birds, almost certainly owls, in this district [North Norfolk] which exhibit a hitherto unrecorded phenomenon. I am inclined to believe that most of the tales respecting "will-of-the-wisps", "corpse-candles", and "lantern-men" are the result of occasional luminosity assumed by birds of nocturnal habits that frequently fly over marshy ground in search of prey. For instance, on February 3, 1907, on reaching the top of Twyford Hill, we noticed a light apparently moving in the direction of Wood Norton, and about a quarter of a mile to the north of us. After moving horizontally backwards and forwards several hundred yards, it rose in the air to the height of forty feet or more; then descended and again went through the same evolutions many times. The light was slightly reddish in the centre, and resembled a carriage lamp for which we at first mistook it. We watched it

The characteristic flat pad of grass is clearly visible at this African Grass-owl nest, sited in wet grassland. These owls breed when grass cover is at its peak, making the nest much more difficult to locate. When the chicks are hatching, the female may sometimes assist them by removing pieces of shell. The fledging period for tytonids varies considerably. Although details are lacking for many species, it seems to be shortest in the grass-owls, as would be expected for ground-nesting birds.

[*Tyto capensis*, Grassland Research Station, near Marondera, Zimbabwe.
Photo: Peter Ginn]





All owls regularly regurgitate pellets. This ejection of a soft "ball" containing undigested remains of food begins at a very early age, and the nest and surrounding area, including the ground below, can sometimes be remarkably littered with such discarded pellets. Analysis of pellets has proved to be the primary source of information on the diet of owls. Not only is the Common Barn-owl the best-studied species in this respect, but its stomach juices are also known to be less acidic than those of most other predatory birds. As a consequence, even very small and delicate bones are preserved intact in its pellets, enabling a wide range of prey species to be identified.

[*Tyto alba alba*,
Ávila, Spain.
Photo: Francisco Márquez]

for twenty minutes and were quite at a loss to ascertain its cause. The light emerged from a covert about two hundred yards distant, flying backwards and forwards across the field, at times approaching within fifty yards of where I was standing. It then alighted on the ground for a few seconds. A slight mist hung over the ground. On another occasion, the evening being dark, the bird issued from a covert. Its luminosity seemed to have increased, and it literally lighted up the branches of the trees as it flew past them, occasionally mounting over their tops. After watching it for about half an hour, it was joined by a companion bird hardly so bright. This kept about one hundred yards behind it, but not constantly."

In Western popular culture some aspects of folklore have been borrowed, particularly the owl as a symbol of wisdom. The owl can also symbolize vigilance, a role it has inherited from the iconography of heraldry, which was often stylized from Common Barn-owls. As symbols of evil omen or just as creatures of the night, owls are popular in visual media such as film. In these various guises owls continue to fascinate man and are a popular collectable today, in everything from fridge magnets to works of art.

Status and Conservation

Tytonid owls reach their greatest diversity in the tropics, to which 12 of the 16 species are confined. Of the four ranging into higher latitudes, the Common Barn-owl occurs widely, while the African Grass-owl extends south to South Africa, and the Australian Masked-owl and the Greater Sooty-owl into southern and south-east Australia respectively. The Eastern Grass-owl is a marginal case, reaching the subtropical north of New South Wales in eastern Australia. Most research on tytonid owls has been centred on temperate populations, where a clearer picture of their status has emerged. Current knowledge of the status of tropical species varies considerably: for example, the Lesser Sooty-owl has now been

found to be abundant within its optimal habitat, whereas the Manus Masked-owl remains virtually unknown.

In the latest review of the world's threatened species, published in 1994, five species are listed as threatened: the Madagascar Red Owl is regarded as Endangered; and the Golden, Manus and Taliabu Masked-owls, as well as the Congo Bay-owl, are considered Vulnerable. To these it may be necessary to add the Lesser and the Minahassa Masked-owls, which are currently listed as Data-deficient, while the Lesser Sooty-owl appears as Near-threatened. Thus, only half of the world's tytonid species can really be considered in any way secure.

Recent fieldwork in the 1990's has led to the rediscovery of three of the rarest species, namely the Taliabu Masked-owl, the Madagascar Red Owl and the Congo Bay-owl, and indeed there are now recent records of all species except the Manus Masked-owl. All of the threatened species appear to be sensitive to habitat destruction, particularly the logging of tropical forest and its effect on the availability of nest-sites and food supply. The recent sightings are, of course, encouraging for the future of these owls, and have resulted from surveys targeted at the remaining areas of extant natural habitats that are known to be centres of avian endemism. Much of this work is co-ordinated through BirdLife International, and a great deal of useful information has been gathered on poorly known species. For the most elusive species, such as the Manus Masked-owl, the main problem for researchers is the inaccessibility of areas of likely occurrence, although this very factor has guarded such areas from human settlement and may prove to be crucial in ensuring the owls' continued survival.

The true rarity of owls can be difficult to assess until extensive survey work is undertaken. In south-east Australia, for example, Greater Sooty-owls and Australian Masked-owls are widespread and in places still occur at optimum levels in suitable, undisturbed habitats. With a clearer picture of their distribution emerging, genuine threats can be identified, particularly the significance of habitat disturbance, especially for sensitive species such as the Greater Sooty-owl. Surveys are also inval-

able in revealing evidence of declining numbers in some regions, as is the case with some populations of Australian Masked-owls.

Some owls that in certain areas are known to be rare and local, and affected by habitat disturbance, can be locally common elsewhere, often utilizing other habitat resources. For example, the Eastern Grass-owl is rare and declining over most of its range in Asia, but in Australia some populations have adapted to the boom-and-bust cycles of prey numbers in arid regions, and in parts of eastern Australia to agricultural changes such as the planting of cane fields supporting large rodent populations. The African Grass-owl is locally common within its range, but in some areas it is scarce, as a result of competition from Marsh Owls, as well as loss of suitable habitat, for instance in South Africa, where its numbers are declining.

The Oriental Bay-owl appears to be genuinely rare throughout its extensive range from Sri Lanka to Yunnan and then on to Borneo and Bali. Records have always been few, but, with no extended field studies of this species attempted to date, it may just be elusive in many areas. Nevertheless, the discovery in 1976 of a small population in south-west India suggests rarity as well as elusiveness in a region where much work had already been done. The lack of recent observations from many areas, for example in Bali, where it was last recorded in 1911, equally leads to the conclusion that it is, at any rate locally, a truly rare owl. It is a forest species, and is probably sensitive to disturbance when this affects nesting and roosting sites, as is also the case with sooty-owls. The far more restricted Congo Bay-owl is also rare, as well as highly localized. Several attempts to find it again following its initial discovery in 1951 were unsuccessful, until it was definitively relocated in the same region in 1996.

Those species extending into temperate regions have demonstrated some tolerance to habitat alteration, but, with the

exception of some races of the Common Barn-owl, such tolerance is limited, and is localized to a few areas. In Australia, the Greater Sooty-owl is considered the least tolerant owl species, and it has become a useful environmental indicator of the effects of disturbance in old-growth forest. The Australian Masked-owl occurs in a broader range of habitats, but is limited by the effects of change in habitat diversity and, consequently, on its hunting and breeding activities. The same can be said for the African Grass-owl, since its numbers in the south of its range are now declining as a consequence of increased habitat destruction.

The range expansion of the Common Barn-owl has been most remarkable, and appears to be limited only by winter temperatures of around zero or a few degrees below. This success has been linked with favourable habitat changes, notably in Europe and North America, through the opening-up of land for agriculture by an increasing human population, as well as gradual long-term warming at higher latitudes, although periods of harsher winters in northern Europe in the last 50 years and less favourable habitat changes in many areas have cut back some established populations. In North America, the species' northern breeding limit has expanded slightly over the last 50 years, reaching regions of southern Canada. While there are parts of its range where the Common Barn-owl is still expanding, it is also apparent that it has had a wide global range for a long time, as demonstrated by the fossil record.

Nevertheless, the status of this wide-ranging species varies from locally common to rare, according to the subspecies under consideration. Following on from the earlier expansion, northern temperate *alba* and *guttata* in Europe and *pratincola* in North America are currently in decline in many regions, and intensive conservation efforts have been required to try to stabilize and increase local populations. However, the extent of temperate popu-

It is easy to understand the long-established fascination that human beings have for owls.

This ranges across all cultures, and is perhaps most widely appreciated with regard to the Common Barn-owl.

This species' ghostly appearance and silent flight, the loud and eerie shrieking and hissing sounds it makes, and its largely nocturnal habits have earned it a myriad of names in the folklore of many languages.

These often betray an association in the human mind with witchcraft, magic and death, but in some areas the species is considered a lucky omen.

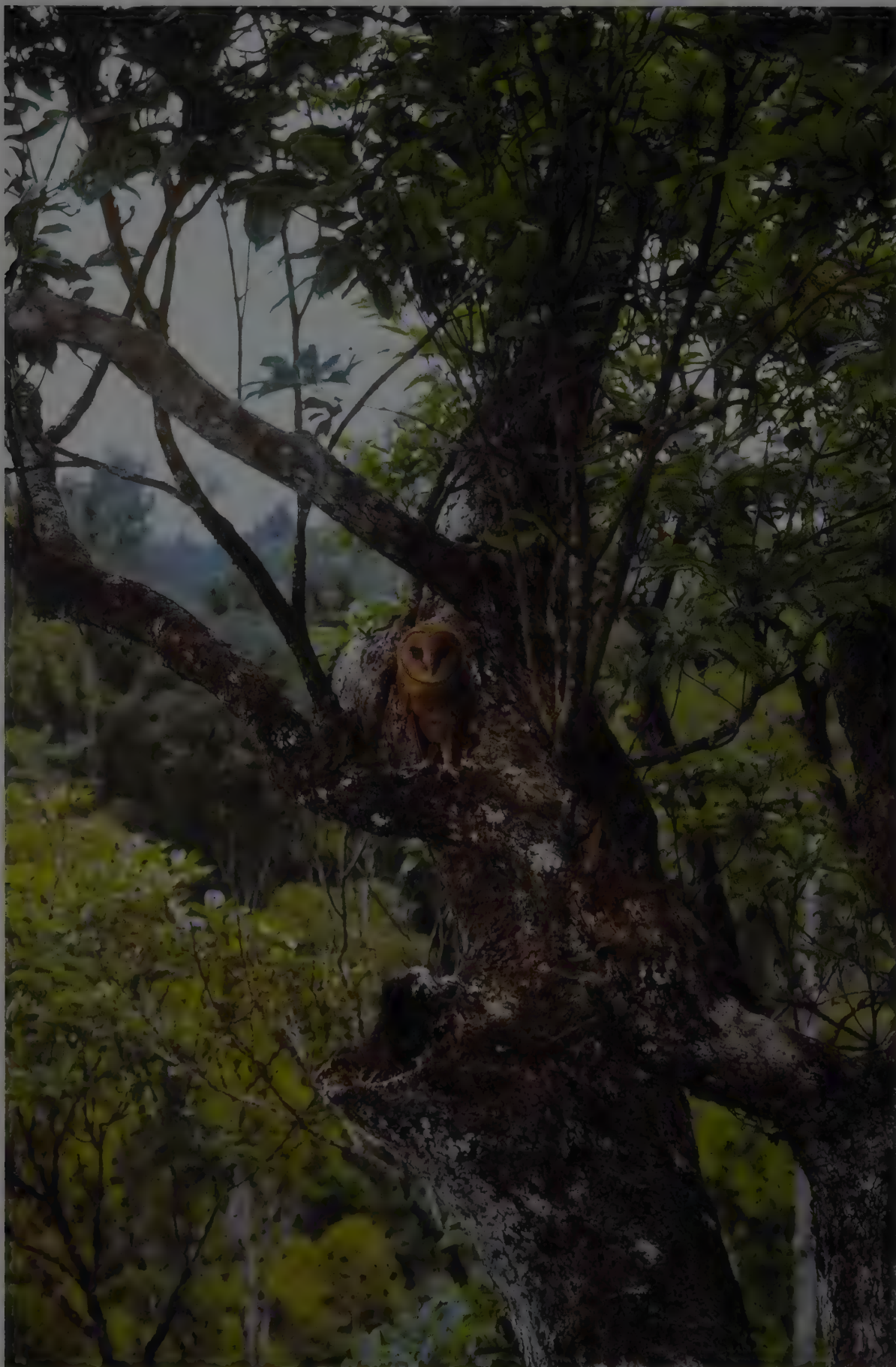
In later centuries, the Common Barn-owl's frequent presence in farmland and around villages added to the superstitions surrounding it, but in more recent times its particular liking for rodents has made it a welcome guest on farms, where it is regarded as a very effective "pest-controller".

[*Tyto alba alba*,

central Ayrshire, Scotland.

Photo: William Paton/
NHPA]





Five of the 16 species of Tytonidae are currently listed as threatened. One of these is the Madagascar Red Owl, which is considered Endangered. Until very recently, there were very few records indeed of this striking owl, and nothing was known of its ecology or biology. Following intensive fieldwork in the 1990's, however, an individual was trapped in October 1994 and fitted with a radio transmitter. This enabled scientists to monitor its movements and to discover, for the first time, some facts about its life. In 1995, this bird nested and raised two young, one of which was then radio-tagged. The Madagascar Red Owls at this study site are to date the only ones to have been studied in the wild. The results have revealed that, among other things, the species inhabits forest edge, that it nests in tree cavities, and that it feeds on small native rodents and insectivores. It is obviously a very rare bird, and has probably always been so within its restricted known range; whether it does in fact have a wider distribution than is realized in Madagascar, but has been confused with the Common Barn-owl (*Tyto alba*), which is widespread on the island, is open to question. Whatever the true situation, the small area in which the species is known to occur is subject to habitat destruction on a scale sufficient to cause concern.

[*Tyto soumagnei*, near Ambanizana, Masoala Peninsula, north-east Madagascar. Photo: Russell Thorstrom]

Not discovered until 1951, the Congo Bay-owl eluded all subsequent attempts to locate it until 1996, when it was rediscovered in the same area in which it had originally been found. It is known from only a single locality in the Itombwe Massif, in easternmost Zaire, where both records have been from montane forest with patches of grassland and bamboo. Two unconfirmed records from sites c. 50 km away, in adjacent Rwanda and Burundi, give some hope that the owl may be slightly less rare than appears.

[*Phodilus prigoginei*,
Itombwe, Zaire.
Photo: Tom Butynski]

lation declines, and their causes and possible solutions, exhibit much regional variation. In contrast to the well-known temperate races, those of lower latitudes are relatively poorly known or quite unknown, and some of them are probably vulnerable, especially those confined to small islands or island groups, often amongst the most distinctive forms. For tropical races, the conservation concerns are the same as for other tropical tytonids, but as mere subspecies of the Common Barn-owl they have attracted less attention, although some may represent separate species (see Systematics). It is worth remembering that only relatively recently was the West Indian Ashy-faced Owl found to be a distinct species, rather than a race of the world's most widespread tytonid.

In both Europe and North America, prolonged and significant declines in Common Barn-owl populations began in many areas as early as the 1930's and 1940's, accelerating in the 1950's and 1960's. In North America, the range expansion of these owls into many areas followed European settlement with its associated forest clearance and agricultural development. Much the same pattern had occurred in much earlier times in Europe. Yet the recent decline of many populations began at around the same time in the two continents and is related to changing agricultural methods, with increasing mechanization, more intensive farming practices and, later, the introduction of organochlorine pesticides, which have now generally been replaced by anticoagulant rodenticides.

Increased efficiency of farming methods has reduced both the diversity and availability of foraging habitats and the numbers of rodents and other prey around storage facilities and other farm buildings. The latter are of particular value to the owls as sources of winter food. Fields have become larger, with the loss of edge habitats, while fertilizers and pesticides have removed the need to rotate crops, with the attendant loss of fallow grassland. Improvements in plant and animal breeding programmes have also reduced habitat variety. Nest-sites have been lost by the removal of natural tree sites and old buildings. The numbers of road-traffic casualties have risen dramatically as more and more roads have been built or extended and traffic speed has increased, particularly where roadside verges had become rich foraging sites.

Conservation programmes have paid special attention to the protection and re-establishment of the habitat mosaics preferred by the owls, with rough grassland, field margins and woodland edges to provide interconnected networks of prey-rich foraging grounds. The focus is on areas large enough not only to support breeding activity but also to ensure survival of as many birds as possible during winter periods, as well as to provide sufficient mobility to reduce possible inbreeding of local populations. The co-operation of farmers and other members of the rural communities is sought as an intrinsic part of the intensive management requirements, in order to sustain the long-term availability of suitable habitat. Where nest-sites have been reduced, nestboxes are provided. The types of box and their locations vary considerably, depending on the needs of particular populations and areas. As they are also used by other bird species, they must be closely monitored and maintained, and cleaned out afterwards, ready for the next nesting. Large numbers of boxes may be necessary simply to ensure that some are used by Common Barn-owls. At one English study site with 37 nestboxes, up to 19% were used for breeding and 47% for roosting, and over 13 years it was found that numbers had not increased but had stabilized; the owls had switched to these safer nest-sites, with the advantage of an increased fledging rate, while any surplus young probably moved to nearby areas.

Conservation programmes are also helped by the resilience of the Common Barn-owl. Mortality rates can be high, as much as 50% to over 70% in Europe, for example, but breeding starts in the first year of life, large clutches are laid, and the young grow rapidly. Losses are quickly replaced, so long as suitable foraging habitat and prey numbers are available. Captive breeding has also been successful, and it was estimated that in 1990, in Britain alone, there were 20,000-30,000 Common Barn-owls in captivity. However, while many of these captive-bred birds were intended for release in the wild, the policy of reintroducing this species is controversial. The effects on existing wild populations have caused some conflict, and the release of 2000-3000 birds annually from the early 1970's to 1992 resulted in high mortal-



ity, with only a few well-organized programmes leading to feral breeding. Since 1992, the release of captive-bred Common Barn-owls has been strictly controlled.

The inadequate regulation and control of rodenticide use is another major concern. While some positive steps are being taken to rectify this in Europe and North America, it has recently been found that Klerat, a second-generation anticoagulant rodenticide registered for use in cane fields in north-east Australia since 1992, has been a principal cause of the subsequent population crash of several species. Numbers of Common Barn-owls, Australian Masked-owls and Eastern Grass-owls, as well as other birds of prey, in that region have dropped by a staggering 75-85%. The effects of pesticides and rodenticides elsewhere urgently need further study, but the Australian case demonstrates the potentially dramatic effects on local populations.

Conservation successes for northern Common Barn-owl populations have resulted from a number of long-term studies. The methods employed may be adaptable to populations of these owls elsewhere, as well as to other *Tyto* species. Knowledge about most tytonid owls, however, currently remains far too sparse. For the tropical forms, as with other tropical bird families, the problems of habitat destruction, particularly the continuing logging of rainforest, together with the impact of human activities such as shooting and trapping, remain major concerns. Since owls are important indicators of the value and biodiversity of natural regions, their role in conservation programmes is of critical importance.

Most people may not see owls as often as they would like, but there can be very few who do not readily enjoy their appearance under a variety of circumstances. The mystery and magic of owls, as well as their importance in natural communities, are reason enough for every effort to be made to ensure their prosperous survival in the future.

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Subfamily TYTONINAE

Genus *TYTO* Billberg, 1828

1. Greater Sooty-owl

Tyto tenebricosa

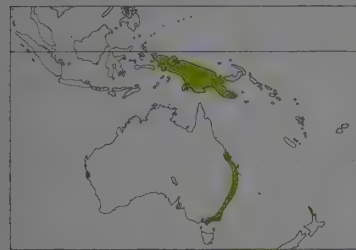
French: Effraie ombrée **German:** Rußeule **Spanish:** Lechuza Tenebrosa
Other common names: Sooty(!)/Black Owl, Dusky Barn-owl

Taxonomy. *Strix tenebricosus* Gould, 1845, River Clarence, New South Wales. Forms superspecies with *T. multipunctata*, and until 1981 treated as conspecific, but differs in size, plumage and voice; these two have occasionally been separated in genus *Megastrix*. Two subspecies recognized.

Subspecies and Distribution.

T. t. arfaki (Schlegel, 1879) - New Guinea and Yapen I.

T. t. tenebricosa (Gould, 1845) - SE Australia from Eungella National Park (EC Queensland) to Dandenong and Strzelecki Ranges (Victoria).



Descriptive notes. Male 37-43 cm, 500-700 g; female 44-51 cm, c. 875-1150 g (*tenebricosa*). When perched, large head and very short tail give "top-heavy" appearance. Darkest of all *Tyto* species, sooty-blackish with small silvery spots; very large black eyes in round facial disc; wings broad and rounded; legs densely feathered, large feet with strong talons. Female as male but larger (1 pair recorded where sizes reversed). Juvenile similar to adult. Race *arfaki* smaller, dark of underparts more variable. **VOICE.** Characteristic contact call a piercing, descending shriek, lasting c. 2 seconds, likened to sound of falling bomb ("bomb

whistle"); given in flight, with periods of minutes to hours between each call; also given in flight or perched by pair in duet-like performance. Other calls include high, piercing trill; also croaks, chirps, rasps, snores, squeals and wheezes, all associated with breeding activity; a screech similar to *T. novaehollandiae* occasionally heard. In New Guinea, descending shriek likened not only to falling bomb, but also to horse's neigh and to whistle of steam kettle. Juvenile utters "tearing calico" screech similar to *T. novaehollandiae* and *T. alba*.

Habitat. In Australia, favours deep, wet gully forest dominated by tall eucalypts, with substorey of rainforest trees and tree ferns, occurring in drier forest only to hunt; in New Guinea to 4000 m, in both lowland and montane rainforest, *Araucaria* pine forest, and recorded above tree-line in boulder-strewn alpine grassland and ridges, occurring in clearings and subalpine grassland only to hunt.

Food and Feeding. Unlike other *Tyto* species, arboreal mammals form bulk of diet, with terrestrial mammals and, rarely, small birds also taken. Size range of prey considerable: from ringtail possums (*Pseudocheirus*) weighing 900 g to mice (18 g); in New Guinea, large scrub-wallabies or pademelons (*Thylagale*) considered to have been taken as carrion. Prey species include gliders and pygmy-possums (Burramyidae/Petauridae), potoroos (*Potorous*), small wallabies (Macropodidae), bandicoots (Peramelidae), small dasyurid marsupials (*Antechinus*, *Sminthopsis*), forest bats, rabbits, large and small rats and mice; also ground thrushes (*Zoothera*), earwigs and beetles. Forequarters of mammals preferred, remainder often discarded; gape large, and skulls often swallowed whole. Hunts inside closed forest in tree tops and on trunks, but also captures prey on forest floor. Although in Australia less inclined to use low perches where ground cover broken, in New Guinea some apparently make regular use of open grassland at higher elevations. Male recorded hunting through forest canopy with female following behind but closer to forest floor, swooping on prey from perch or in flight. In disturbed habitats, particularly logged areas, ratio of terrestrial prey higher, with more hunting in open areas, including roadsides. Able to hunt in total darkness.

Breeding. Jan-Sept, most laying earlier, peaking around Apr. Single-brooded; may not nest each year. Appears to pair for life. Strongly territorial, territory size c. 200-800 ha; nest usually in large hollow of living tree, 0.5-5 m deep and at height of 10-50 m, also in rock crevices and caves, particularly large caves with nest cavity high above floor; some tree sites occupied for up to 9 years, and sites probably used for longer periods by same or several pairs; 1 cave site recorded as occupied for c. 10,000 years (based partly on analyses of accumulated debris, including remains of prey species long extinct in region); no nest made, but pellets and other debris may be used for egg placement. Clutch 1-2 eggs, usually 2, laid c. 4 days apart, usually with 1 chick surviving; incubation c. 35 days; natal down white to sooty-grey, second (mesopile) down sooty-grey; young fledges after c. 60 days, dependent on parents for further 4-5 months, usually returning to nest-site to roost for first few weeks. In captivity, greater reproductive potential has been noted: with ample food supply, can breed at any time, raise 2 broods per year with up to 3 young per brood, and breed when 1 year old.

Movements. Essentially sedentary. In Australia, movements of breeding pairs relate to habitat disturbance and fragmentation, particularly effect of reduced prey abundance. Juvenile post-breeding dispersal may account for a ringing recovery of a bird wandering 50 km, partly across cleared areas, though apparently unusual, as failure to disperse over open country may explain absence from suitable areas in W & C Victoria and lack of inland vagrant records. Recent records from EC Queensland, N of Conondale Range, indicate more N distribution limit than generally accepted, probably representing small, scattered resident populations rather than northward vagrancy. However, records from EC Queensland could still result from some dispersal of non-breeding birds. Old reports of occurrence on Flinders I, in Bass Strait, where species was considered resident; however, these records now considered erroneous, as referring to Morepork (*Ninox novaeseelandiae*).

Status and Conservation. Not globally threatened. CITES II. In Australia, not so much rare as seldom recorded. Recent results of surveys indicate a widely distributed owl probably at optimum levels in suitable habitat, but declining where habitat disturbed; in New South Wales, recent decline estimated at c. 20%. Total Australian population recently estimated at 2000-7000 pairs.

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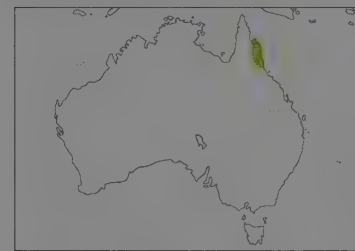
2. Lesser Sooty-owl

Tyto multipunctata

French: Effraie piquetée **German:** Fleckenrußeule **Spanish:** Lechuza Moteada
Other common names: Sooty Owl(!), Silver Owl

Taxonomy. *Tyto tenebricosa multipunctata* Mathews, 1912, Johnstone River, north Queensland. Forms superspecies with *T. tenebricosa*, and until 1981 treated as conspecific, but differs in size, plumage and voice; now usually recognized as separate species, though occurring between the ranges of the two races of *T. tenebricosa*; these two species have occasionally been separated in genus *Megastrix*. As recently as 1940, present species was considered not to differ even subspecifically from *T. t. tenebricosa*. Monotypic.

Distribution. NE Queensland, from Cedar Bay S to Paluma and inland to Windsor, Atherton and Evelyn Tablelands.



Descriptive notes. Male 31-35 cm, 430-450 g; female 35-38 cm, 540 g. Plumage silvery and blackish, paler below, upperparts and wing-coverts with numerous silvery spots; paler facial disc with very large, dark eyes; short tail. Smaller and paler than *T. tenebricosa*, upperparts more densely spotted, and underparts lighter, silvery white with pattern of dark chevrons on pale background, especially on breast; legs and feet proportionately smaller. Sexes similar, including foot proportions. Juvenile similar to adult. **VOICE.** Calls similar to *T. tenebricosa* but higher-pitched, thinner and more penetrating, and birds generally noisier.

Piercing, downscale "bomb whistle" contact call, often with slight step in smooth downward progression, given in flight and when perched, usually when approaching nest with food and when leaving nest area.

Habitat. Rainforest, mainly above 300 m, rarely to sea-level, occurring in disturbed habitats and clearings only to hunt.

Food and Feeding. Prey includes pygmy-possums and small gliders (Burramyidae/Petauridae), and small dasyurid marsupials; arboreal and particularly terrestrial rodents, including water rats (*Hydromys*); medium-sized forest birds, including catbirds (*Ailuroedus*, *Scenopoeetes*), riflebirds (*Ptiloris*) and chowchillas (*Orthonyx*); and beetles and earwigs. Like *T. tenebricosa* is an efficient hunter within closed forest, but making greater use of low perches, commonly sides of tree trunks, and taking more prey on ground; also uses rainforest tracks and clearings. Able to hunt in total darkness and during heavy rainfall.

Breeding. Dates variable, depending on rainfall; eggs can be laid in any month, mostly Mar-May; territorial pairs may miss a season if conditions unfavourable. Nest-site usually large hollow, up to c. 40 m above ground, in trunk or main limb of living tree, commonly *Eucalyptus grandis*, but recently found also to use several species of rainforest tree, e.g. crevice in strangler fig (*Ficus*); depth of hollow varies from level with entrance to several metres deep; no nest made, eggs laid on pellet and other debris. Clutch usually 2 eggs, occasionally 1; incubation c. 40-42 days; natal down white to sooty-grey, second (mesopile) down sooty-grey; young fledge after c. 90 days, known to remain in breeding territory for at least several weeks.

Movements. Sedentary. Post-breeding dispersal of juveniles may explain lower-altitude and off-shore sightings. Vagrant to Hinchinbrook I. Recent report of record from W New Guinea an error for *T. tenebricosa*.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Queensland Wet Tropics EBA. Currently considered Near-threatened. Within total world range of c. 4000 km², population recently estimated at c. 2000 breeding pairs. Abundant within optimal habitat; territories as small as 50 ha, some nests only c. 400 m apart.

Bibliography. Anon. (1994g), Barker & Vestjens (1989), Blakers *et al.* (1984), Britton (1990a, 1990b, 1991), Burnett *et al.* (1996), Christidis & Boles (1994), Condon (1975), Fleay (1979, 1981), Garnett (1993), Higgins (1999), Hollands (1991, 1995), Lindsey (1992), Macdonald (1988), Mathews (1912a, 1916), Mees (1964), Olsen (1998), Palliser (1985), Pizzey & Doyle (1998), Pizzey & Knight (1997), Rothschild & Hartert (1913), Schodde & Mason (1981, 1997), Schodde & Tidemann (1986), Simpson & Day (1998), Stattersfield *et al.* (1998), Stewart (1984), Storr (1984), Strahan (1994), Trounson & Trounson (1987), Whittle (1994).

3. Australian Masked-owl

Tyto novaehollandiae

French: Effraie masquée **German:** Neuhollandeule **Spanish:** Lechuza Australiana
Other common names: Chestnut-faced/Maw-faced/Masked/Cave Owl; New Guinea Masked-owl (*calabyi*); Tasmanian Masked-owl/Owl (*castanops*)

Taxonomy. *Strix*? *Nova Hollandiae* Stephens, 1826, New South Wales.

Forms superspecies with *T. aurantia*, *T. manusi*, *T. sororcula*, *T. nigrobrunnea* and *T. inexpectata*. Some authors treat *T. sororcula* and *T. manusi* as conspecific with present species, and in part most of the above allopecies were lumped into present species. Race *castanops* often treated as separate species, but recent review of size and colour variation within S Australian populations supports

inclusion within present species, at subspecific level. New Guinea population *calabyi* has been proposed to constitute a megasubspecies, but again differences do not seem sufficiently marked. Race *galei* sometimes merged with *kimberli*, as observed differences may not be consistent and few specimens have been used in analyses. Birds of SW Western Australia may merit separation as distinct race, due to significantly larger size, but more study needed; formerly separated in race *perplexa*. Cave-dwelling population of South Australia might be separable as race *troughtoni*, but remains very poorly known. Six subspecies currently recognized.

Subspecies and Distribution.

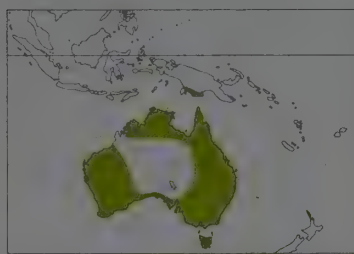
T. n. calabyi Mason, 1983 - S New Guinea, in S Trans-Fly region, from Merauke area to Tarara and Daru I.

T. n. melvillensis Mathews, 1912 - Melville I and Bathurst I (off N Australia).

T. n. galei Mathews, 1914 - NE Cape York Peninsula in NE Queensland, from Pascoe R to Chester R. *T. n. kimberli* Mathews, 1912 - N Australia from Yampi Peninsula E to S Cape York Peninsula and Atherton Tablelands.

T. n. novaehollandiae (Stephens, 1826) - SW Western Australia E to Victoria and N to NE Queensland (Townsville), mainly in discontinuous and coastal distribution, but also scattered inland records, mostly from E Australia.

T. n. castanops (Gould, 1837) - Tasmania and Maria I; also Maatsuyker I, where perhaps only vagrant. Introduced (*castanops*) to Lord Howe I.



Descriptive notes. Male 33-42 cm, 420-800 g; female 38-57 cm, 545-1260 g. Occurs in dark and light colour morphs, with variation within each, and with intermediates. Dark morph has upperparts blackish-brown, washed rufous and speckled white, underparts pale rufous, coarsely spotted dark, and facial disc dark chestnut; light morph has upperparts pale grey, washed yellow and speckled dark and white, underparts white, sparsely grey-flecked, and facial disc white. Light morph confusable with *T. alba*, but often more distinctly spotted below, with rounder and more strongly margined facial disc, more densely feathered and heavier legs, larger feet

with massive talons, and stronger and more purposeful flight (unlike lighter, slightly erratic flight of *T. alba*); *T. longimembris* has longer legs with protruding feet in flight, longer wings, more heart-shaped facial disc, black and orange upperparts and terrestrial habits. Female always much bigger than male and sometimes twice as heavy. Juvenile similar to adult or more heavily spotted. Nomininate race generally dark morph or intermediate; *castanops* female always dark, while male may have paler, but never white, breast; *kimberli* generally light or intermediate; largest birds in Tasmania (female largest of all congeners), averaging smaller northwards, *galei* smallest; *melvillensis* also small and apparently all dark or intermediate; *calabyi* as dark on upperparts as nominate, with larger legs, and wings paler, like *galei*, but longer. **Voice.** Various calls, mostly associated with breeding, include cackles, chatters, shrieks, rasps, squeals and hisses; richer, louder and deeper than those of *T. alba*. Characteristic is a very loud, shrill scream, lasting 1-2 seconds, given once only soon after dusk, usually in flight, after leaving nest-site, but variations may be given 1-4 hours after dusk, or similar calls of longer duration by male during circling courtship flight.

Habitat. Usually associated with tall open forest dominated by big trees suitable for nesting and roosting; unlike *T. tenebrosica*, favours sites with access to more open areas. More numerous where greatest local forest and woodland diversity occurs, i.e. forest types with dry, open understorey, providing variety of dense and sparse ground cover. Smaller numbers patchily distributed away from coastal regions in wooded farmland, riparian woodland and isolated stands of large trees; also pine plantations, and in N Australia *Melaleuca* swamps and mangrove edges; in S Australia, relict population has adapted to treeless plains, using caves and rock clefts for nesting and roosting.

Food and Feeding. As for *T. tenebrosica*, wide weight range of prey from large possums to mice. Includes possums (*Trichosurus*, *Pseudocheirus*), gliders and pygmy-possums (*Burrardidae*/Petauridae), potoroos (*Potorous*), bandicoots (*Peramelidae*), dasyurid marsupials, rabbits, rats and mice; also records of domestic fowl, kookaburras (*Dacelo*), Australian magpies (*Gymnorhina*), House Sparrows (*Passer domesticus*), reptiles, beetles and large moths. While some arboreal species taken, most prey captured on ground, by hunting both on wing and from perches; after dusk, changes from low hunting flights over open ground to perch-hunting.

Breeding. May breed at any time of year; most eggs laid Mar-Jul, N birds earlier, Tasmanian birds later. Apparently territorial, pair-members may stay together all year; in SE Australia, estimated territory size c. 1000-1200 ha; nest-site a large hollow 40-500 cm deep in living or dead tree, at height of 12-25 m, usually in trunk but also in vertical branch spout; favours isolated trees or trees higher than surrounding ones, with same sites used for many years (over 20 kg of pellet material removed from 1 site); in Nullarbor Plain region of S Australia, nesting recorded on cliff ledge and in cleft of caves; no nest constructed, but few instances of male making depression in debris in hollow and once even adding a few sprigs of eucalypt leaves. Clutch 2-4 eggs, usually 2; incubation 35-42 days; natal down white, second (mesopile) down creamy; young fledge after 10-12 weeks, still with traces of down, stay near nest for several weeks, repeatedly calling at night for food, and may use nest as daytime roost.

Movements. Sedentary. Only movements may be post-breeding dispersal of juveniles, and opportunistic exploitation by adults of recently disturbed habitats or changes in prey abundance, including rodent plagues, but not to extent of *T. alba* and *T. longimembris*. In SW Australia, some records attributed to seasonal movements but possibly due to post-breeding dispersal or unrecorded breeding.

Status and Conservation. Not globally threatened. CITES II. Breeding pairs found at 1-10 km intervals, and in N Queensland 5 pairs within 30 km; recent surveys in SE Australia have demonstrated wider range and incidence of records, though in New South Wales population has halved and in Victoria only 300-400 breeding pairs estimated to remain. Status of "Cave Owl" population of Nullarbor Plain unknown, but probably very few, if any, remain; decline possibly result not only of human persecution and loss of prey species earlier in 20th century, but also of competition with *T. alba*; latter also widely recorded from Nullarbor region and current status there also unknown, but remains of both species found at same site in 1984 (and evidence of diets) suggests that some degree of niche overlap may account for presence of both owls. Still widespread in Tasmania, but numbers declining; probably only vagrant on Maatsuyker I. Apparent rarity in SW Australia may be due to under-sampling. In N Queensland, rodenticides used since 1992 for rat control in cane fields have caused local population declines of 75-85%.

Bibliography. Baker-Gabb (1993), Barker & Vextjens (1989), Beehler *et al.* (1986), Beruldsen (1980), Blackhall (1995), Blakers *et al.* (1984), Bright (1992), Britton (1990a, 1990b, 1991, 1992), Carter (1977), Christidis & Boles (1994), Clark *et al.* (1978), Coates (1985), Collins (1995), Condon (1975), Cooper & McAllan (1995), Davey (1993), Debus (1990, 1993a, 1993b, 1994a, 1995, 1997a, 1997c), Debus & Rose (1994), Emison *et al.* (1987), Fleay (1949, 1979, 1981), Ford (1968, 1986), Francis (1992), Fullager *et al.* (1974), Garnett (1993), Green, R.H. (1982, 1989, 1995), Higgins (1999), Hill (1955), Hollands (1971, 1991, 1995), Hutton (1991), Hyem (1979),

Kavanagh (1996, 1997), Kavanagh & Bamkin (1995), Kavanagh & Murray (1996), Kavanagh & Peake (1993a, 1993b), Kavanagh, Debus, Tweedie & Webster (1995), Lindenmayer (1996), Long (1981), Mason (1983), Mathews (1912a, 1916), Mayr (1941a), McAllan (1997), McAllan & Bruce (1989), McNabb (1992), Mees (1963, 1964, 1982b), Mooney (1992, 1993, 1997), Napier (1969), Newgrain *et al.* (1993), Olsen (1998), Olsen & Marples (1993), Palliser (1985), Parker (1977b), Peake *et al.* (1993), Press *et al.* (1995), Rand & Gilliard (1967), Roberts (1983), Rothschild & Hartert (1913), Rounsevell *et al.* (1977), Saunders, D.A. & Ingram (1995), Saunders, P. (1995), Schodde & Mason (1981, 1997), Schulz (1987), Sharland, M. (1981), Sharpe (1875), Skemp (1955), Stewart (1984), Storr (1977, 1980, 1984, 1985a, 1985b, 1987, 1991), Storr & Johnstone (1985, 1988), Strahan (1994), Thomas, D.G. (1979), White (1985), Young & De Lai (1997).

4. Golden Masked-owl

Tyto aurantia

French: Effraie dorée

German: Goldeule

Spanish: Lechuza Dorada

Other common names: Bismarck Masked-owl, Golden Owl, Golden/New Britain Barn-owl

Taxonomy. *Strix aurantia* Salvadori, 1881, New Britain.

Forms superspecies with *T. novaehollandiae*, *T. manusi*, *T. sororcula*, *T. nigrobrunnea* and *T. inexpectata*. Monotypic.

Distribution. New Britain.



Descriptive notes. 27-33 cm. Distinguished from other masked-owls by its golden-buff plumage, darker above, paler below, with blackish-brown mottling. Female similar to male but larger. Juvenile undescribed. **Voice.** Calls attributed to this owl are a "ka-ka", repeated c. 6 times per second and ascending slightly, and a long ascending whistle heard at night at same locality.

Habitat. Rainforest, from lowlands to c. 1830 m.

Food and Feeding. Stomach of 1 specimen contained a small rodent.

Breeding. Undescribed.

Movements. Presumably sedentary.

Status and Conservation. VULNERABLE. CITES II. Restricted-range species: present in New Britain and New Ireland EBA. Considered rare, with few recent field records, including sightings in 1978 and 1984 in forest-edge habitat. Species is probably adversely affected by continuing forest destruction. Research and census work urgently required.

Bibliography. Clark *et al.* (1978), Coates (1985), Collar & Andrew (1988), Collar *et al.* (1994), Gilliard & LeCroy (1967a), Gurney (1882, 1894), Meyer (1934), Salvadori (1881), Schodde (1978), Stattersfield *et al.* (1998).

5. Manus Masked-owl

Tyto manusi

French: Effraie de Manus

German: Manuseule

Spanish: Lechuza de la Manus

Other common names: Manus Owl, Admiralty Islands Masked-owl

Taxonomy. *Tyto manusi* Rothschild & Hartert, 1914, Manus, Admiralty Islands.

Forms superspecies with *T. novaehollandiae*, *T. aurantia*, *T. sororcula*, *T. nigrobrunnea* and *T. inexpectata*. Sometimes considered conspecific with *T. novaehollandiae*. Evidence of extinct populations from Mussau and New Ireland may refer to undescribed races of present or closely related species, perhaps also isolated on single islands, and suggests that masked-owls may once have occurred more widely in Bismarck Archipelago. Monotypic.

Distribution. Manus I, in Admiralty Is.



Descriptive notes. c. 33 cm. Distinguished from other masked-owls by combination of dark upperparts, rufescent brownish buff underparts with large blackish spots, and black tail with narrow, irregular, yellowish-brown bars. Type specimen, collected 1913, is male with wing 275 mm, compared with second known specimen, a female with wing 301 mm, indicating that, as with other masked-owls, female is larger than male. Juvenile plumage undescribed. **Voice.** Undescribed.

Habitat. Rainforest; perhaps confined to hilly terrain at higher elevations (Manus I reaches 702 m).

Food and Feeding. Undescribed.

Breeding. Undescribed.

Movements. Presumably sedentary.

Status and Conservation. VULNERABLE. CITES II. Restricted-range species: present in Admiralty Islands EBA. No recent records. Failure to find this owl during a 1990 survey suggests that it is confined to areas away from human settlement (not visited during survey), possibly explaining its unfamiliarity to local inhabitants, who occupy coastal areas, access inland being limited to a single road in E Manus. Type specimen was collected near a coastal settlement, suggesting population decline since 1913, although numbers probably always small. Further research and census work required.

Bibliography. Buckingham *et al.* (1995), Coates (1985), Collar *et al.* (1994), Dutson & Newman (1991), Rothschild & Hartert (1914), Stattersfield *et al.* (1998), Steadman & Kirch (1998), Stresemann (1933, 1934).

6. Lesser Masked-owl

Tyto sororcula

French: Effraie des Tanimbar

German: Molukkeneule

Spanish: Lechuza de las Tanimbar

Other common names: Tanimbar Owl

Taxonomy. *Strix sororcula* P. L. Selater, 1883, Larat, Tanimbar Islands.

Forms superspecies with *T. novaehollandiae*, *T. aurantia*, *T. manusi*, *T. nigrobrunnea* and *T. inexpectata*. Sometimes treated as conspecific with *T. novaehollandiae*. Race *cayeli* may repre-

sent a separate species; Seram population may represent an undescribed race. Species name often misspelt *sororcula*. Two subspecies recognized.

Subspecies and Distribution.

T. s. cayellii (Hartert, 1900) - Buru; also Seram (probably this race).

T. s. sororcula (P. L. Slater, 1883) - Tanimbar Is (Larat, Yamdena).



Descriptive notes. c. 29-31 cm. Nominate race is smallest member of masked-owl group; upperparts brownish, mottled white, underparts whitish with dark spotting on sides, and pale legs covered only with flesh-coloured bristles. Female apparently as male but larger. Juvenile undescribed. Race *cayellii* averages slightly larger, and is generally more tawny buff over all of plumage; upperparts more blackish, mottled brownish, with white mottling only on wing-coverts, and narrowly black-barred yellowish-brown tail. **VOICE.** Undescribed.

Habitat. Presumably rainforest (Buru, Seram) and primary and mature secondary monsoon

forest (Tanimbar).

Food and Feeding. Undescribed.

Breeding. Undescribed.

Movements. Presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Banda Sea Islands EBA and Buru EBA. Data-deficient. Apparently rare, and no current data on numbers or localities. On Buru, lowland areas cited by collectors of 2 extant specimens. Kaleji Bay (1889) and Wae Eno (1921), now much altered and doubtless unsuitable; while a 1989 survey did not record this species, additional surveys are under way on Buru and new data may soon be forthcoming. Also, no precise locality for 2 specimens known from Tanimbar Is (1882 and 1923), but apparently suitable habitat still extensive; although 1985 and 1993 surveys on Yamdena failed to locate this owl, it was sighted there in late 1995, and a proposal for an integrated conservation and development project on Yamdena is currently being assessed. Details of a *Tyto* owl discovered on Seram in 1987 hitherto limited to photographic evidence, and exact identity remains to be determined, but it probably represents an undescribed subspecies of present species.

Bibliography. Andrew (1992), Anon. (1996e), Bishop (1989), Coates & Bishop (1997), Collar & Andrew (1988), Collar *et al.* (1994), Hartert (1929), Inskipp *et al.* (1996), Isherwood *et al.* (1998), Monk *et al.* (1997), Poole (1996), Siebers (1930), Stattersfield *et al.* (1998), Stresemann (1933, 1934), Sujatnika *et al.* (1995), White & Bruce (1986).

7. Taliabu Masked-owl

Tyto nigrobrunnea

French: Effraie de Taliabu

German: Taliabueule

Spanish: Lechuza de la Taliabu

Other common names: Taliabu Owl/Barn-owl, Sula Owl/Masked-owl, Black-brown Owl

Taxonomy. *Tyto nigrobrunnea* Neumann, 1939, Taliabu, Sula Islands.

Forms superspecies with *T. novaehollandiae*, *T. aurantia*, *T. manusi*, *T. sororcula* and *T. inexpectata*. Until recently, often considered conspecific with *T. inexpectata*. Monotypic.

Distribution. Taliabu, in Sula Is.



Descriptive notes. c. 32 cm. Male unknown, presumably similar to female. Unique type specimen, female, has upperparts dark brown with lines of small white spots, wings and tail dark brown with no bars; facial disc pinkish-brown, darker around eyes; underparts golden-brown, thinly vermiculated with black and covered with black spots. Juvenile unknown. **VOICE.** Undescribed.

Habitat. Presumably rainforest; also sighted recently in selectively logged lowland forest, which perhaps enters only to hunt.

Food and Feeding. Undescribed.

Breeding. Undescribed.

Movements. Presumably sedentary.

Status and Conservation. VULNERABLE. CITES II. Restricted-range species: present in Banggai and Sula Islands EBA. Presumed to be scarce; a few recent sight records, including 1 standing on a dirt road. Effects of ongoing habitat destruction unknown. No existing protected areas in Sula Is, where remaining forest covered by timber concessions. Research and census work urgently required.

Bibliography. Andrew (1992), Bishop (1989), Coates & Bishop (1997), Collar & Andrew (1988), Collar *et al.* (1994), Davidson *et al.* (1995), Eck & Busse (1973), Holmes & Philipps (1996), Inskipp *et al.* (1996), Monk *et al.* (1997), Neumann (1939), Stattersfield *et al.* (1998), Stones, Davidson & Raharjaningirah (1997), Sujatnika *et al.* (1995), White & Bruce (1986).

8. Minahassa Masked-owl

Tyto inexpectata

French: Effraie de Minahassa

German: Minahassaeule

Spanish: Lechuza de Minahassa

Other common names: Minahassa/Unexpected Owl/Barn-owl

Taxonomy. *Strix inexpectata* Schlegel, 1879, Minahassa, Sulawesi.

Forms superspecies with *T. novaehollandiae*, *T. aurantia*, *T. manusi*, *T. sororcula* and *T. nigrobrunnea*. Until recently, widely considered to include *T. nigrobrunnea* as a race. Species name often misspelt *inexpectata*. Monotypic.

Distribution. N & NC Sulawesi.



Descriptive notes. c. 30 cm. Upperparts mixed black and rusty with no white speckling or spotting, wings barred black and rufous; facial disc tinged light rusty; underparts light rusty with variable black spotting. Differs from *T. alba* in smaller size, slimmer shape, smaller facial disc in relation to body size. Juvenile apparently has browner wings, and underparts greyish-white and speckled. **VOICE.** Described as similar to that of *T. rosenbergii* but weaker and less deep.

Habitat. Primary and lightly disturbed hill and lower montane forest and disturbed riverine forest, occasionally forest edge, at 100-1500 m.

Food and Feeding. Undescribed.

Breeding. Evidence of breeding in early Apr; juvenile apparently being fed by adults in early to middle Sept 1995. One probable nest hole was in *Elmerrillia* tree; fledged juvenile was attended by adults c. 25 m up in strangler-fig tree.

Movements. Presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Sulawesi EBA. Data-deficient. Known only from 11 specimens and 3 sightings from 5 localities, all but 1 from N Sulawesi; only other locality is in Lore Lindu National Park S of Palu at 675 m, where a specimen was found dead in Nov 1980. Original source localities of most specimens greatly altered and presumably no longer contain suitable habitat, though later records indicate populations in more secure forest areas, notably Dumoga-Bone National Park. Sparsely distributed and rare, or just overlooked; perhaps locally common where its optimal habitat can be surveyed.

Bibliography. Andrew (1992), Andrew & Holmes (1990), Bishop (1989), Coates & Bishop (1997), Collar & Andrew (1988), Collar *et al.* (1994), Fletcher (1998), Holmes & Philipps (1996), Inskipp *et al.* (1996), van Marle (1940), Rozendaal & Dekker (1989), Stattersfield *et al.* (1998), Stresemann (1940), Sujatnika *et al.* (1995), Watling (1983), White & Bruce (1986), Whitten *et al.* (1987).

9. Sulawesi Owl

Tyto rosenbergii

French: Effraie des Célèbes

German: Sulawesieule

Spanish: Lechuza de Célebes

Other common names: Sulawesi/Celebes Masked-owl/Barn-owl, Rosenberg's Owl/Barn-owl, Celebes Owl

Taxonomy. *Strix rosenbergii* Schlegel, 1866, Modelido, Boni and Gorontalo, Sulawesi.

Recently considered part of masked-owl group, but apparently more closely related to *T. alba*. Race *pelengensis* frequently misspelt "*pelelensis*". Two subspecies recognized.

Subspecies and Distribution.

T. r. rosenbergii (Schlegel, 1866) - Sulawesi and Sangihe.

T. r. pelengensis Neumann, 1939 - Banggai Is (Peleng).



Descriptive notes. 43-46 cm. Male upperparts dark blackish-grey with white speckling and white spots; facial disc dusky white to brownish; underparts buffy with blackish spots and darker feather edges; tail with 5 black bars. Female darker, with heavier spotting on underparts, which tends to form bars. Juvenile undescribed. Race *pelengensis* markedly smaller, with broken black feather edges on chest, giving scaly appearance. **VOICE.** A very hoarse, dry screech with slight hissing quality, usually given in flight; eerie, long, shrill "skkeear" uttered occasionally when hunting at or after dusk.

Habitat. Lightly wooded cultivation, tall dead trees in open country, grassland, forest edge and young coconut plantations; occasionally around villages and urban areas; from sea-level to 1200 m. Hunts over clearings and cultivation, forest edge, and after dark along roads; rarely seen during day.

Food and Feeding. Recorded feeding on rats; pellets collected in a cave chamber on Sulawesi and attributed to present species contained rats, shrews and a bat (*Hipposideros*), and evidence of possible nestling cannibalism.

Breeding. Undescribed.

Movements. Presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Widespread but generally uncommon in Sulawesi, though fairly common locally in Palu Valley; present in Dumoga-Bone National Park. Status on Sangihe and Peleng unknown. Research and survey work required.

Bibliography. Andrew (1992), Andrew & Holmes (1990), Catterall (1997), Coates & Bishop (1997), Coomans de Ruiter & Maurenbrecher (1948), Hartert (1929), Holmes & Philipps (1996), Inskipp *et al.* (1996), Neumann (1939), Riley (1997a), Rozendaal & Dekker (1989), Schlegel (1866), Sharpe (1875, 1876), Stresemann (1940), Watling (1983), White & Bruce (1986), Whitten *et al.* (1987).



10. Common Barn-owl

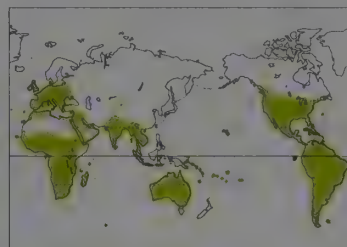
Tyto alba

French: Effraie des clochers **German:** Schleiereule **Spanish:** Lechuza Común
Other common names: Barn Owl, Lesser Masked-owl(!), Monkey-faced Owl, Cave/Death/Delicate/Demon/Ghost/Golden/Hissing/Night/Screech/Silver/White Owl; Eastern/Australian Barn-owl (*delicatula*); Galapagos Barn-owl (*punctatissima*)

Taxonomy. *Strix alba* Scopoli, 1769, Friuli, Italy. Up to 46 races recognized in recent works, but status and distribution of several uncertain, and review of whole group long overdue. West Indian taxa *glaucoops*, *insularis* and *nigrescens* formerly included in present species, now shown to be separate species. *T. glaucoops*; some authors separate only *glaucoops*, retaining other two races in present species. Considerable variation in size and colour may be more individual than geographical in many continental and some island regions, with possibly expanding zones of intergradation, particularly in Europe. Nominate and *guttata* intergrade from Netherlands, Belgium and N & E France to Germany (Rhine Valley) and C Switzerland; nominate intergrades with *affinis* in region of S Egypt and N Sudan. Validity of many proposed races considered too doubtful to be upheld: in Europe, *pusilla*, *kleinschmidt*, *kirchhoffi* and *hostilis* merged with nominate, and *rhena* with *guttata*; Madagascan *hypermetra* with African *affinis*; island populations *everetti*, *kuehni*, *bellonae*, *lifuensis* and *lulu* with widespread Australasian *delicatula*; Bahamian *luayana* with *pratincola*; and, in Neotropics, Colombian *subandana* with *guatemalae*, *stictica* with *contempta* and *hauchecornei* with *tuidara*. Also, current separation of *niveicauda* from *furcata* (based on colour characters) and of *guatemalae* from *pratincola* (ranges in Central America not yet satisfactorily determined) perhaps doubtful, and continued separation of *bondii* may not be tenable; size and colour variation in Neotropics in need of reassessment, and separation of *hellmayri* from *tuidara* based on size characters questionable. Furthermore, *poensis* possibly not separable from *affinis*, in which case *poensis* (as older name) has priority over latter. N African nominate race birds sometimes placed in *erlangeri*; birds from S Myanmar to Indochina sometimes placed in *javanica*, but seem better included in *stertens*. Melanesian populations, currently covered by 3 races (*delicatula*, *crassirostris*, *interposita*), may merit further splits. Several well-marked insular races (e.g. *detorta*, *thomensis*, *deroepstorffii*, *punctatissima* and possibly others) may be separate species; recent proposals to elevate *delicatula* to species level (see page 36), however, do not consider which races it would include. Twenty-eight subspecies currently recognized.

Subspecies and Distribution.

T. a. alba (Scopoli, 1769) - W & S Europe (including Balearic Is and Sicily) to N Turkey; also W Canary Is (Tenerife, Gran Canaria, El Hierro), and N Africa from Morocco to Egypt (except Sinai), S to N Mauritania, S Algeria, Niger (Air Massif) and NE Sudan.
T. a. guttata (C. L. Brehm, 1831) - C Europe E to Latvia, Lithuania and Ukraine, and SE to Albania, Macedonia, Romania and NE Greece.
T. a. ernesti (Kleinschmidt, 1901) - Sardinia and Corsica.
T. a. erlangeri W. L. Slater, 1921 - Crete and smaller S Greek islands, Cyprus and patchily from Syria E to SW Iran and S to NE Egypt (Sinai) and S Arabian Peninsula.
T. a. schmitzi (Hartert, 1900) - Madeira and Porto Santo.
T. a. graciliorstris (Hartert, 1905) - E Canary Is (Fuerteventura, Lanzarote, Lobos, Montaña Clara, Alegranza).
T. a. detorta Hartert, 1913 - Cape Verde Is.
T. a. affinis (Blyth, 1862) - Africa S from S edge of Sahara, including Zanzibar and Pemba, and Madagascar and Comoro Is.
T. a. poensis (Fraser, 1842) - Bioko I.
T. a. thomensis (Hartlaub, 1852) - São Tomé I; recorded in error from Príncipe I.
T. a. stertens Hartert, 1929 - Indian Subcontinent S to N Sri Lanka, and E to SC China (Yunnan), Vietnam and S Thailand.
T. a. deroepstorffii (Hume, 1875) - S Andaman Is.
T. a. javanica (J. F. Gmelin, 1788) - Malay Peninsula S to Greater Sundas (including Krakatau, Pulau Seribu and Kangean Is, and possibly S Borneo) and E to Alor, as well as Tanahjampea, Kalao and Kalaotoa.
T. a. sumbaensis (Hartert, 1897) - Sumba I.
T. a. meeki (Rothschild & Hartert, 1907) - E New Guinea and nearby islands of Manam and Karkar.
T. a. delicatula (Gould, 1837) - Sawu, Roti(?), Timor, Jacor, Wetar, Kisar and Tanimbar Is; Australia and offshore islands; Long I and possibly N New Britain and New Ireland; also Nissan, Buka, Solomon Is (including Bougainville), S Vanuatu (Erromanga, Tanna, Aneityum), New Caledonia, Loyalty Is, Fiji (N to Rotuma), Tonga (N to Niao'ou), Wallis and Futuna Is, Niue I, Western Samoa and Samoa.
T. a. crassirostris Mayr, 1935 - Tanga Is (E Bismarck Archipelago).
T. a. interposita Mayr, 1935 - Santa Cruz Is, Banks Is, N Vanuatu (S to Efate).
T. a. pratincola (Bonaparte, 1838) - S Canada S at least to Mexico; also Bermuda, Bahamas and Hispaniola.
T. a. guatemalae (Ridgway, 1874) - Guatemala and perhaps S Mexico to Panama (including Pearl Is), possibly to W Colombia.
T. a. bondii Parkes & Phillips, 1978 - Bay Is (Roatán, Guanaja), off N Honduras.
T. a. furcata (Temminck, 1827) - Cuba, Cayman Is and Jamaica.
T. a. niveicauda Parkes & Phillips, 1978 - I of Pines.
T. a. bargei (Hartert, 1892) - Curaçao, and possibly also Bonaire.
T. a. punctatissima (G. R. Gray, 1838) - Galapagos Is.
T. a. contempta (Hartert, 1898) - W Venezuela, Colombia (except W?), Ecuador and Peru.
T. a. hellmayri Griscom & Greenway, 1937 - E Venezuela (including Margarita I) through the Guianas to N Brazil (S to Amazon); also Trinidad and Tobago.
T. a. tuidara (J. E. Gray, 1829) - Brazil (S of Amazon) S to Tierra del Fuego and Falkland Is. Introduced (*affinis*) to Seychelles; also (*delicatula*, *pratincola*) to Lord Howe I, where now presumed extirpated (few records since 1970's considered vagrants); also (*pratincola*) to Hawaii.
Descriptive notes. 29-44 cm; 187-455 g (Europe, N Africa), 266-470 g (S Africa), 400-700 g (North America), 387-558 g (Surinam), 264 g (Galapagos Is); male av. 555 g, female av. 612 g (Malaysia); male 227-418 g, female 220-475 g (Australia). Medium-sized, long-legged owl with distinctive heart-shaped face. Nominative race golden-buff above, with variable light greyish "veil", and finely streaked, mottled and dotted dark; white facial disc and underparts, sometimes with pale buff on sides of chest and/or fine spotting on breast and flanks; legs densely feathered; eyes dark; buoyant, slow, wavering flight, with legs dangling, appears ghost-like. No similar owl over much of range (but in Afrotropics race *affinis* overlaps with *T. capensis* and from India to Australia *stertens* and *delicatula* with *T. longimembris*, both those species longer-legged and usually notably darker, also in Australia with *T. novaehollandiae*, which usually larger and darker but some more like present species). Female like



male, tends to be slightly darker. Juvenile similar to adult, or more heavily spotted. Racial variation considerable, from light grey to buff above and from white to buff below, with varying amount of black spotting and speckling, but widespread intergradation (common in Europe and tropical regions), and island races tending to be smaller and with either whiter or buffier plumage (but some isolated, dark tropical island races): *guttata* grey, sometimes buff-washed, above, buff (male) to rufous-buff (female) and usually spotted below; *ernesti* pale and white-breasted; *erlangeri* also white-breasted, but upperparts more golden; *schmitzi*, *graciliorstris* and *detorta* buff-breasted, darkest in *detorta*; *affinis* greyer above than nominate, with more and coarser spotting below; *poensis* similar, but darker above, more golden-buff and streaked and speckled black and white, primaries barred and tail buffier; *thomensis* smaller, much darker, dark grey above with conspicuous small black and white spots, golden-brown below; *stertens* pale and greyish above, with small spots on pale underparts; *javanica* similar but more golden-buff above, larger spots below; *deroepstorffii* smaller, darker, with dark brown upperparts, deep brownish-rufous underparts; *sumbaensis* slightly larger than *javanica*, larger bill, almost white tail with narrow black bars; *meeki* like *sumbaensis* but tail bars paler, bill smaller, underparts silvery-white with arrow-shaped dusky spots; *delicatula* like *javanica*, but brownish-grey to light grey above, mottled pale brown with slight tawny tint, white below, 4 brown bars on tail; *crassirostris* darker, bill and feet more robust; *interposita* washed orange-ochre; *pratincola* upperparts vary from pale orange-buff to lighter or darker grey mixed with orange-buff, underparts white to pale orange, spotted or vermiculated brown (similar to European birds but larger, with stronger legs and feet); *guatemalae* like darker *pratincola*, but more uniform above, more coarsely speckled below (extent of differentiation from *pratincola* indeterminate); *bondii* apparently smaller and paler than *pratincola*; *furcata* pale orange-buff above with greyish-brown spots, white below with few flank spots; *niveicauda* averaging whiter and paler than *furcata*; *bargei* like nominate, but smaller, with shorter wings; *punctatissima* small, dull brown above with few scattered dusky white spots, golden-buff to white below with brownish vermiculations or fine dense spots; *contempta* black above with fine pale grey mottling and white spots at feather tips, pale rusty-brown below with irregular black cross-markings, but characters variable; *hellmayri* larger than *tuidara*, both dark to pale yellowish above and near-white to golden-buff below, with or without dusky spotting. VOICE. Diverse range of calls associated with breeding, including screeches, wheezes, purrs, snores, twitters, hisses and yelps; less vocal at other times; also bill-snapping, tongue-clicking and wing-clapping. Male's familiar screech, considered advertising or warning call, usually given in flight, a hoarse, screaming, eerie "shrrreeeee" with gargling or rattling quality and tremulous effect (from wing action), of c. 2-3 seconds' duration, repeated after 1-20 seconds, often many in series, but usually singly when patrolling territory; female's variant lower-pitched, more broken, especially when both call during aerial chases. Variations of other loud screams and screeches attributed to mobbing response or distress behaviour.

Habitat. Occurs in great variety of habitats according to availability of prey, seasonality in temperate regions, and competition from other predators; in higher latitudes limited by severity of winters, rarely occurring N of areas with mean Jan temperature around or few degrees below 0°C. Prefers open lowlands with some trees, including farmland with hedges, ditches, ponds and banks, roadside verges and related rougher terrain, and young conifer plantations; also around towns, suburbs, villages or more isolated buildings suitable for daytime roosts and nest-sites; sometimes near refuse dumps. In lower latitudes, also semi-arid and some arid regions with xerophytic vegetation, dwarf shrub and herb communities, deciduous or mixed eucalypt woodland, *Acacia* savanna, thornbush, heathland, open marshes, mudflats, oil palm plantations, irrigation areas, rice paddies and cane fields, and cliffs and rocky coasts in some regions, notably on continental offshore islands; some darker island races also in forest; on small tropical islands in all available habitats. Usually lowlands, but at higher altitudes in many areas, up to c. 4000 m.

Food and Feeding. Diet better studied than that of any other raptor, most extensively in Europe and North America but also in Israel, parts of Africa (particularly S Africa) and South America (Galapagos Is, Chile, Argentina, Surinam), Australia, and a few other localities. In major sample studies, 74-100% (in most cases 90-100%) of diet small mammals, usually dominated by only few species, especially rats and mice; in Europe and North America also voles (Cricetidae), gophers (Geomysidae) and shrews (Soricidae); in Africa also shrews, other Insectivora and gerbils (Gerbillinae); in South America also small opossums (Didelphidae); in Australia also bandicoots (Peramelidae), dasyurid marsupials and gliders (Burramyidae/Petauridae). Other mammals include young rabbits and hares (Leporidae), moles (Talpidae), bats, and skunks, stoats and weasels (Mustelidae). Also birds, particularly communally roosting passerines, e.g. thrushes (Turdidae), starlings (Sturnidae), sparrows (Passeridae), weavers (Ploceidae) and finches (Fringillidae), but vast range of other birds in small numbers or of local importance, from seabirds (Procellariidae, Hydrobatidae, Sternidae, Alcidae), small herons (Ardeidae), kestrels (*Falco*), young megapodes (Megapodidae), quails (Phasianidae), domestic fowl, buttonquails (Turnicidae), rails (Rallidae), plovers (Charadriidae), small waders (Scolopacidae), to pigeons (Columbidae), lorikeets (Psittacidae), cuckoos (Cuculidae), swifts (Apodidae), kingfishers (Alcedinidae) and small woodpeckers (e.g. *Colaptes*), and wide range of passerines from at least 12 families. Other prey lacertid and agamid lizards, skinks (Scincidae), geckos (Gekkonidae), chameleons (Chamaeleonidae), slow-worms (*Anguis fragilis*) and grass snakes (*Natrix natrix*); frogs (Anura) and toads (Bufonidae); small fish, e.g. trout (*Salmo*), roach (*Rutilus*), carp (Cyprinidae), rudd (*Scardinius erythrophthalmus*), perch (*Perca*) and grunion (*Leuresthes tenuis*); larger insects, e.g. grasshoppers (Saltatoria), beetles (Coleoptera), mantises (Mantidae), moths (Lepidoptera), wasps (Hymenoptera) and termites (Isoptera); spiders (Arachnida) and scorpions (Scorpionida); littoral isopods (Isopoda); earthworms (Annelida); and rarely carrion. Much non-mammalian prey caught incidentally or opportunistically, but can constitute significant part of diet in some tropical and semi-arid regions, e.g. lizards and invertebrates in parts of Africa and on some islands. Discarded eggshells and faeces of smaller nestlings may also be eaten; occasional chick cannibalism at nest, victim usually dead from unknown causes, but young recorded killed and eaten by siblings. In some temperate regions, when main prey species scarce or absent, many starve rather than switch to alternatives; this also occurs in boom/bust cycle of rat and mouse plagues, when excess production of young leads to many often starving. Hunts close to ground in searching flight, undulating and hovering, diving on to prey with talons extended, usually from height of c. 3 m, also commonly from perch; either method used by same bird, or one more than other, depending on habitat type, e.g. perch-hunting predominant in denser vegetation. Normally strictly nocturnal, with high auditory acuity in locating prey in complete darkness. Daylight hunting regular in Scotland and England and well known on various Pacific islands; also observed elsewhere, e.g. W USA (Utah) and Surinam, though extent unknown; may be widespread if owls

not mobbed when they appear. Normally hunts singly; sometimes many together during prey plagues, e.g. in Australia, where often joined by *T. longimembris*, *T. novaehollandiae* and other raptors.

Breeding. In tropics can start in almost any month, generally late in dry season, in more arid areas during wetter periods; in N temperate regions mostly Mar-Jun, when double-brooded mostly Mar-May and Jun-Aug, initial activity varying among habitats; in some temperate regions season correlated with cycles of prey abundance, but similar from year to year where highly dependent on more homogeneous agricultural landscapes; in South Africa after rains, Feb-May in summer rainfall regions and Aug-Dec in winter rainfall region of SW Cape, but can breed in any month depending on local conditions; in Australia opportunistic according to food supply, can be at any time of year, most peaking Mar-Jun and Aug-Nov; May-Aug in New Caledonia, 1 or 2 broods, rarely 3 (e.g. in Malaysia), depending on food supply; exceptionally, 4 (Zimbabwe) within 11 months during mouse plague, with first egg of next clutch laid while chicks still in nest. Monogamous, but polygamy sometimes recorded, rarely polyandry and incest; territorial, but loosely colonial nesting recorded in USA; sometimes near other owls, e.g. in Scotland 34-40 m from Tawny Owl (*Strix aluco*) and in USA in association with Great Horned Owl (*Bubo virginianus*); in captivity, hybridization recorded between male of present species and a female Striped Owl (*Asio clamator*), 2 of 4 eggs fertile and developing until 15th day. Site a natural cavity in tree trunk, stump or large hollow branch, 2-20 m above ground, or in cliff or bank, including sea-cliffs and small, exposed islands, in cave, walls of lava tubes, even in ground; also in hollow of palm tree; wide diversity of artificial structures with adequate room and access also used (e.g. old church, tower, castle, ruin, barn, abandoned building, loft, dovecote, windmill, disused water tank, arched bridges and other large structures, lighthouse, chimney, haystack, duckblind, unused boat, up to 10 m down in abandoned well); also purpose-built nestboxes and those used in rat-control programmes (e.g. in Malaysia); burrows c. 1 m deep in cliffs and banks may be wholly or partially excavated; also uses large abandoned nest, e.g. of Osprey (*Pandion haliaetus*), in Africa of Hamerkop (*Scopus umbretta*) and communal nests of Sociable Weaver (*Philetairus socius*); sometimes takes over occupied nest, e.g. in Scotland wool-lined stick nest of Eurasian Jackdaw (*Corvus monedula*) in chimney, yet also recorded sharing active site with latter; some sites used over multiple seasons; either no nest or slight scrape or depression, with pellets and other debris as insulating layer. Clutch 2-16 eggs, usually 4-7, laid 2-3 or more days apart; if first clutch lost, replacement usually smaller; incubation 29-34 days; male's only involvement is in feeding female and young; natal down white, second (mesoptile) down white, creamy-white or buffish-cream; nestling period 7-10 weeks; young dependent on parents for further 3-5 weeks, then disperse within 2-8 weeks. Most hatched chicks survive; in South Africa, record of 12 chicks successfully reared from a single nesting attempt. Can breed in less than 1 year.

Movements. Most populations sedentary, with post-breeding dispersal of juveniles, as well as some movement of adults where prey numbers fluctuate. Data from Europe and North America indicate considerable regional variation, particularly after high prey abundance. In Scotland most disperse within 20 km; in C Europe 50-100+ km to W & S, with a few ringing recoveries 1200-1600 km distant; Dutch-ringed young moved c. 1500 km to Spain and Ukraine; nominate race vagrant to Azores, *guttata* to Jan Mayen I, S Scandinavia and S Finland, each also vagrant within other's range. In America, *pratincola* from N USA move generally farther, 80-320 km, with recoveries at up to 1760 km; in S USA most disperse within 80 km, but recoveries at 248 km and 984 km indicate that wide dispersal not entirely due to severe winter weather; wanders or strays seasonally to Newfoundland, S Alaska, Tres Marias and Revillagigedo Is off W Mexico, Cuba, Hispaniola, Puerto Rico, Jamaica and Central America. Reported evidence of migration in NE USA suggested as flocking behaviour associated with post-breeding dispersal. Middle Eastern race *erlangeri* vagrant to NE Iran/Transcaspia region. Movements of Afrotropical *affinis* include 1000 km from Senegambia to Sierra Leone and 579 km and 400 km within S Africa. Indian/Indochinese race *stertens* may be merely vagrant to SC China (Yunnan), though recent sources suggest rare resident there; records from southernmost Thailand since 1970's may be N-moving *javanica* rather than *stertens* (*javanica* formerly only vagrant W of Java, with spread as breeding bird only since 1960's). Movements of 65-840 km recorded for *delicatula* in SE Australia, where some populations highly nomadic, with irruptions associated with rodent plagues, as well as seasonal movements to N areas for dry season (winter) and away from coasts in summer, doubtless accounting for long-distance vagrancy to Norfolk and Lord Howe Is and New Zealand. However, several New Zealand records are of birds transported in undercarriage bays of aircraft (1, dead on arrival, apparently from USA), and some may originate from Fiji; the 7 or 8 records include 1 on Little Barrier I, Jun-Oct 1992. Race *delicatula* also irregular visitor to Tasmania and Bass Strait islands and vagrant to Houtman Abrolhos off W Australia. In S South America *tuidara* has occasionally reached Falkland Is, where breeding first reported 1989; also on South Georgia, where evidence of breeding observed in 1998. Over-water dispersal is obvious source of many vagrants; several records of owls landing on ships up to 360 km from land suggest some vagrancy ship-assisted, e.g. a New Jersey bird recovered in Bermuda (c. 1250 km), where first bred 1931; also sightings on offshore oil rigs. In some tropical areas inter-island movement common, e.g. in smaller island groups of Fiji. Unidentified dark *Tyto* owls recently observed on several Fiji islands, if not vagrant *T. longimembris*, could be dark-morph birds of present species, hitherto unknown from Fiji.

Status and Conservation. Not globally threatened. CITES II. Status of many populations uncertain, particularly those on islands, but others locally common; species expanding in some areas, especially temperate regions, as a result of increases in availability of suitable habitats and artificial nest-sites. Formerly occurred N to S Scandinavia, and small numbers have been reintroduced to S Finland; recently extinct in Malta, where last bred in 1988; has also disappeared from Aldabra; recorded in error from Austral Is and Society Is; recent breeding records in Falkland Is. Current European population 110,000-230,000 breeding pairs, with c. 90% of nominate race and two-thirds of total in just 2 countries (France and Spain); densities of up to c. 25 pairs/50 km² but generally much lower, especially in E Europe. Far greater densities attained in some nestbox programmes, e.g. on oil-palm estates in Malaysia; species first discovered nesting in Peninsular Malaysia in 1969 on an oil-palm estate, where many owls had been attracted to large population of rats feeding on oil palms; few nest-sites were available, but owls responded well when nestboxes provided; in 1988, attempt at biological control of rats, with 200 nestboxes erected for present species in 1000 ha of oil palms near Kuala Lumpur; by late 1989, 95% of boxes occupied, giving density of c. 1 pair/5 ha, and offering alternative to use of second generation rodenticides; species now common throughout Malay Peninsula. Nestboxes used as part of local conservation efforts in Europe and North America, where N populations have been declining for c. 50 years; causes of decline include loss and fragmentation of grassland foraging habitat, intensification of agricultural practices since 1940's, urbanization, and road development, with attendant upsurge in road mortalities, all coupled with increasingly harsh winters during that period. Increased mechanization of farms has meant loss of important foraging sites, such as stackyards and stables, and loss of abandoned farm buildings suitable for nest-sites. Organochlorine pesticides in 1950's and 1960's and rodenticides in 1970's and 1980's had disastrous effects on many owl populations in Europe, particularly NW Europe, and parts of North America; in NE Australia, rodenticides used since 1992 for rat control in cane fields have caused local population declines of 75-85%. Conservation efforts have also included protection and re-establishment of rough-grassland habitat mosaics, providing prey-rich foraging areas, and controls over use of second-generation anticoagulant rodenticides; reintroduction schemes in some areas have had mixed success, as well as conflicting with wild populations. While mortality rates in temperate regions can be very high, birds start breeding in first year, lay large clutches, young grow rapidly, and losses can quickly be replaced, so long as

suitable habitat, prey abundance and nest-sites exist. Most die within 1-2 years, but ringing returns have demonstrated that small numbers survive for up to 21 years.

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11. Ashy-faced Owl

Tyto glaucops

French: Effraie d'Hispaniola **German:** Hispaniolaschleiereule **Spanish:** Lechuza de la Española
Other common names: Hispaniolan/Ashy-faced Barn-owl

Taxonomy. *Str[ix] glaucops* Kaup, 1853, Jamaica; error = Hispaniola.

Until recently considered conspecific with *T. alba*. Following colonization of Hispaniola in late 1970's by *T. a. pratincola*, latter found not to interbreed with nominate *glaucops*, and separation as two species now widely accepted. Several recent works consider nominate *glaucops* part of a natural group including *insularis* and *nigrescens* (last 2 forms possibly comprising a separate species, *T. insularis*), with extinct form *T. cavatica* from intervening island of Puerto Rico also considered closely related to this group; others place *insularis* and *nigrescens* in *T. alba*. On present evidence, best option may be to treat the three extant races as one species, with *cavatica* probably representing an extinct race. Limited available data suggest similarities to small island races of *T. alba* that may also warrant treatment as separate species. Colour characters of race *nigrescens* may not be tenable. Three subspecies tentatively recognized.

Subspecies and Distribution.

T. g. glaucops (Kaup, 1853) - Hispaniola, including Tortue I.

T. g. nigrescens (Lawrence, 1878) - Dominica.

T. g. insularis (Pelzelin, 1872) - St Vincent, Bequia, Union, Carriacou and Grenada.



Descriptive notes. 26-43 cm. Nominat race has distinctive silvery-grey facial disc, dark greyish-brown upperparts with light brown and dusky vermiculations, mixed with buff or tawny mottling on wings, and tawny underparts with some transverse barring. Occurs in light and dark morphs, with intermediates. Sexes similar, but female slightly larger. Juvenile has darker grey face. Race *insularis* has vinaceous-brown facial disc, blackish-grey upperparts sparsely spotted or streaked white, darker wings mottled and edged tawny, cinnamon-buff underparts mottled dusky with some small white spots; *nigrescens* like *insularis*, but almost lacks white spotting above and has less mottling below. **VOICE.** A hissing cry, prefaced by a series of higher-pitched ratchety clicks and a screeching call likened to "criiissssh" recorded for Hispaniola. On Dominica, a piercing scream and a loud clicking sound recorded. Other calls may be similar to some calls of *T. alba*. **Habitat.** Open woodland, forest, scrub and caves; also agricultural areas, abandoned buildings, villages and towns; from lowlands to over 2000 m. **Food and Feeding.** Mainly small mammals, including rats, mice and small bats; also birds, including domestic fowl, doves (Columbidae), cuckoos (Cuculidae), swifts (Apodidae), hummingbirds, (Trochilidae), trogons (Trogonidae), todies (Todiidae), woodpeckers (Picidae), swallows (Hirundinidae), thrushes and solitaires (Turdidae), Palmchats (*Dulus dominicus*), weavers (Ploceidae), vireos (Vireonidae), finches (Fringillidae), New World warblers (Parulidae) and tanagers (Thraupidae); anolis lizards (Iguanidae); and tree frogs (Hylidae). Nocturnal hunter, foraging habits similar to those of *T. alba*. **Breeding.** Eggs in Sept on Dominica; nestlings Apr; main season Jan-Jun on Hispaniola. Natural cavity nest-sites, including hollow trees and branches, sinkholes, also cave ledges, and artificial sites similar to those of *T. alba*. Clutch 3-7 eggs; no other data.

Movements. Sedentary; extent of post-breeding dispersal unknown.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Hispaniola EBA. Widespread and locally common on Hispaniola; in Dominican Republic said to be common, particularly in S parts. Status of Lesser Antillean races insufficiently known, but *nigrescens* appears to be common on Dominica, whereas *insularis* is rare on St Vincent and Grenada and in Grenadines.

Bibliography. Anon. (1989c, 1998a), Bond (1928a, 1928c, 1942, 1949, 1956a, 1978, 1979, 1985, 1987), Clark *et al.* (1978), Dod (1987), Hartert (1929), Hill (1964), Lack & Lack (1973), Lack *et al.* (1973), Olson (1978), Raffaele *et al.* (1998), Ridgway (1914), Sharpe (1875, 1876), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Wetmore & Swales (1931).



12



13



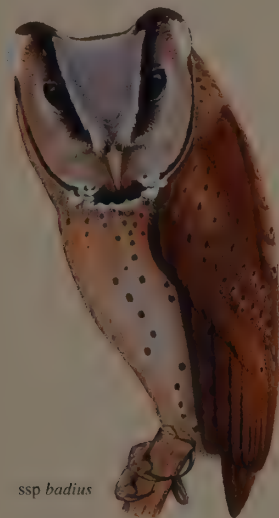
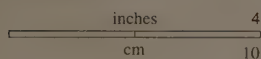
14

ssp *longimembris*



ssp *chinensis*

PLATE 3

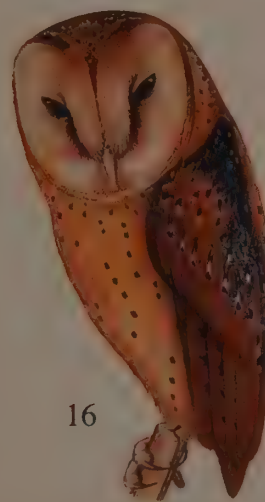


ssp *badius*

15



ssp *saturatus*



16

PLATE 3

Family TYTONIDAE (BARN-OWLS) SPECIES ACCOUNTS

12. Madagascar Red Owl

Tyto soumagnei

French: Effraie de Soumagne **German:** Malegasseneule **Spanish:** Lechuza Malgache
Other common names: Madagascar Grass-owl/Masked-owl, Soumagne's Owl

Taxonomy. *Heliophilus Soumagnei* Milne-Edwards, 1878, Madagascar.

Close relative of *T. alba* group, of which it constitutes a small, dark, island form. Sufficiently differentiated, however, always to have been regarded as a separate species, and indeed sometimes a separate genus, *Heliophilus*. Monotypic.

Distribution. NE & E Madagascar.

Descriptive notes. 27.5-30 cm; 323 g. Plumage suffused orange-red, darker above and paler below, with fine black spots; facial disc greyish-buff, darker around eyes; eyes blackish. Sexes similar.

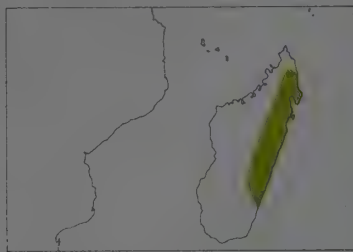
Juvenile similar to adult, but initially brighter. **Voice.** Loud, eerie, hissing screech, "shreeee", dropping towards end, similar to that of *T. alba* but higher-pitched and more vigorous; also "wok wok wok" or "wac-wac-wac..." calls, and a single, explosive call or brief resonant alarm.

Habitat. Traditionally linked with undisturbed rainforest at 900-1200 m, but recent studies indicate forest edge, rice paddies and other cultivation important, at least for hunting, and day roosts found in small ravines among bananas and secondary growth. Radio-tagged bird trapped at sea-level, frequented lowland secondary growth and open areas subjected to human disturbance, roosting during day in secondary vegetation. Forages in forest and nearby open areas.

Food and Feeding. Almost exclusively small native mammals (insectivores and rodents), especially shrewlike tenrecs (*Microgale*), rice tenrecs (*Oryzomys*) and tuft-tailed rats (*Eliurus*), in size range 13-72 g; also occasional rats (*Rattus*) and old report of frogs. No information on feeding behaviour; strictly nocturnal, and recorded singly or in pairs.

Breeding. Only 1 nest described: site c. 23 m above ground in natural tree cavity; 2 recently hatched young Sept; natal down white, developing noticeable facial disc at 1 month; fledged Nov-Dec at 10

On following pages: 13. African Grass-owl (*Tyto capensis*); 14. Eastern Grass-owl (*Tyto longimembris*); 15. Oriental Bay-owl (*Phodilus badius*); 16. Congo Bay-owl (*Phodilus prigoginei*).



weeks, and remained in natal area for at least c. 4 months.

Movements. Apparently sedentary; radio-tagged bird was sedentary over 15 months, nesting 2 km from original roosting area of a year earlier.

Status and Conservation. ENDANGERED, CITES I. Restricted-range species: present in East Malagasy Wet Forests EBA. Old records from Sihanaka forest and Masoala Peninsula; sighting in 1973 near Andasibe was first record in wild since 1934; 1 found in captivity in Aug 1993 at Andapa, in Anjanaharibe Sud Special Reserve, c. 300 km N of known range. Individual trapped in Oct 1994 in Masoala Peninsula was radio-tagged and monitored until Dec 1995 using radio telemetry; had home range of 210 ha; in Sept 1995 it nested and raised 2 young, 1 of which was fitted with a transmitter and observed through Mar 1996, 4 months after it had fledged. Probably always uncommon within restricted range, much of which is threatened by habitat destruction; true distribution and status, however, possibly clouded by confusion with *T. alba*, which is widespread and relatively common throughout Madagascar. Intensive research and conservation urgently required.

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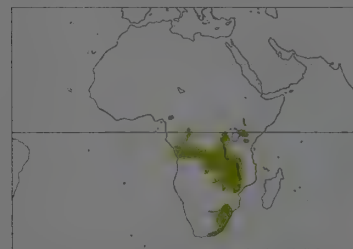
13. African Grass-owl

Tyto capensis

French: Effraie du Cap **German:** Kapgraseule **Spanish:** Lechuza de El Cabo
Other common names: Grass Owl(!), Cape/Common Grass-owl, Cape/African Owl

Taxonomy. *Strix Capensis* A. Smith, 1834, Cape Town, South Africa.

Forms superspecies with *T. longimembris*, and often treated as conspecific. Some minor variation recorded, but races *damarensis*, *libratus* and *cameroonensis* considered no longer tenable. Monotypic. **Distribution.** Cameroon highlands (3 records); Congo and N Angola E to S Uganda and W Kenya, then S through W Tanzania and Zambia to W Mozambique and E South Africa (formerly W to Cape Town); single record from Ethiopia; recorded in error from Namibia.



Descriptive notes. 34-37 cm; 266-520 g. Dark sooty olive-brown upperparts with white dots contrast distinctly with whitish to pale buff underparts with dark spots; facial disc pale buff to whitish; eyes small, dark; bill creamy. Larger and darker than *T. alba*; confusable, particularly in marshy areas, with Marsh Owl (*Asio capensis*), but latter has dark face and underparts, more rounded wings, darker (less white) underwing, is less nocturnal and retracts legs when flushed (present species dangles legs). Sexes alike. Juvenile darker above without white spots, with more rufous facial disc, and darker buff below. **Voice.** Similar to *T. alba*, but less strident, more muted screeches; soft, cricket-like "tik-tik-tik..." given on wing; high-pitched, sibilant tremolo of 1-2 seconds also noted; nestlings utter snake-like hiss.

Habitat. Open grassland, vleis, marshes and lush moist grassland up to 3200 m; also open *Acacia* woodland. By day roosts in nest or separate tunnel structure, in pairs or groups of up to 5 birds; uses same roost regularly, when birds may extend tunnels up to 1-5 m long to connect with other tunnels.

Food and Feeding. Prey includes rodents, especially vlei rats (*Otomys*), also shrews (Soricidae), hedgehogs (Erinaceidae), elephant-shrews (Macroscelididae), young hares (Leporidae), bats, birds up to size of crakes (Rallidae) and snipe (*Gallinago*), reptiles, frogs, dung beetles and termites; weight range of prey 1.5-120 g; also eats eggshells. Pellet studies have shown that rodents comprise 76-98% of diet. Hunts in low, quartering flight, usually starting earlier in evening and finishing later in morning than *T. alba*; at grass fires, hunts rodents escaping from flames.

Breeding. Breeds at time of greatest grass cover: Oct-Jul in South Africa; Nov-May, mainly Feb-Apr, in Zimbabwe; Feb-Jun in Malawi and Zambia; Apr, with nestlings recorded Jan, Mar and Aug, in Zaire; and Aug-Mar in E Africa. Nest usually near or under a bush, a flattened pad of grass at end of grassy tunnel in dense tuft, also connected to other tunnels running through grass which can be used for escape by adults and young (if old enough) if nest invaded by predator. Clutch 2-5 eggs, rarely 4; incubation 32-42 days, eggs hatching within 24-hour period or on consecutive days; natal down white, second (mesopile) down buff or pale golden-brown; young fledge in c. 42 days, but stay near nest for further c. 30 days.

Movements. Sedentary. Some local movements likely, depending on food supply, as well as post-breeding dispersal of juveniles; Ethiopian record perhaps of juvenile. Possible vagrant to W Gambia.

Status and Conservation. Not globally threatened. CITES II. Most numerous in E Africa; sparsely recorded in C Africa; locally common in Zambia, Malawi, Zimbabwe and Mozambique; local and uncommon in South Africa, where numbers declining through habitat destruction. Scarcity in many areas is also attributed to competition with *Asio capensis*, which is commoner (ratio 9:1), although the two species are recorded sharing roost-sites.

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14. Eastern Grass-owl

Tyto longimembris

French: Effraie de prairie **German:** Graseule **Spanish:** Lechuza Patilarga
Other common names: Grass Owl(!), Australasian Grass-owl

Taxonomy. *S[trix] Longimembris* Jerdon, 1839, the Nilgiris, near Coonoor, India.

Forms superspecies with *T. capensis*, with which often considered conspecific. Variation within species poorly understood, owing to rarity of specimens from whole range. Several other forms previously separated racially (*walleri*, *oustalei*, *maculosa*) now included in nominate *longimembris*, although Australian *walleri* perhaps warrants recognition due to plumage differences and sexual dimorphism; Guangxi Zhuang and Guangdong population (*melli*) merged with *chinensis*; *chinensis* itself sometimes included in *pithecopis*, but probably better retained as separate race. Six subspecies recognized.

Subspecies and Distribution.

T. l. longimembris (Jerdon, 1839) - India, S Nepal, Bangladesh and Myanmar; Sulawesi, Tukangbesi Is (Kaledupa), Flores, Sumba and N, C & E Australia.

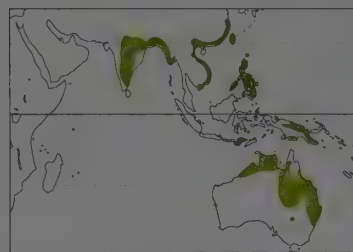
T. l. chinensis Hartert, 1929 - SE China (SE Yunnan to Jiangsu) and Vietnam.

T. l. pithecopis (Swinhoe, 1866) - Taiwan.

T. l. amaurota (Cabanis, 1872) - Philippines.

T. l. baliem Ripley, 1964 - W New Guinea (Baliem Valley, Snow Mts).

T. l. papuensis Hartert, 1929 - E New Guinea (C & SE ranges, Huon Peninsula).



Descriptive notes. Male 32-36 cm, 265-375 g (Australia), 360 g (Philippines); female 35-38 cm, 320-450 g (Australia), 582 g (Philippines). Male dark brown and golden-buff above with some small white spots; facial disc and underparts contrastingly whitish, tinged orange-buff, underparts with sparse blackish dots; flight feathers barred dark, with golden-buff patch at base of primaries; tail pale, barred dark; eyes dark. Darker than sympatric races of *T. alba*; generally not so dark as *T. capensis*. Female as male, or with darker face and underparts. Juvenile resembles adult female, or darker. Australian birds ("walleri") slightly buffier and on

average with more dorsal and ventral spotting, could be confused with light-morph *T. novaehollandiae*; race *chinensis* entirely suffused tawny-buff, but some paler; *pithecopis* larger, with some buff suffusion; *amaurota* like nominate, but slightly larger, upperparts more greyish, buff areas more yellowish, tail bars wider, female and juvenile with facial disc washed vinaceous-brown; *papuensis* upperparts plainer, darker grey with narrow white shaft streaks, not spots (but some nominate also with streaks), size approaching or equalling *pithecopis* and *amaurota*; type (adult male) of *baliem* described as having upperparts much darker than *papuensis* and extending to 2 dark patches on sides of neck, possibly averages smaller. **Voice.** In Asia noted to have screech like *T. alba*, but generally more silent. Various calls recorded in Australia: hissing scream in flight over breeding grounds, with loudness and harshness intermediate between *T. alba* and *T. novaehollandiae*; cricket-like chirruping by male returning to nest with food, audible only at close range, highly sibilant "psseoo" in flight near nest (perhaps alarm call); another possible alarm near nest is harsh "scaarp, scaarp" by female; also bill- or tongue-snapping, and snoring and high-pitched trilling or wheezing calls by nestlings.

Habitat. Grassland, both tall grass jungle and open grassland, paperbark (*Melaleuca*) savanna, marshes, floodplains and heathland, particularly when undisturbed by human activity, but also cultivated and cleared areas, including cane fields; in Australia, recently young pine plantations. In many regions, prefers grassy hillsides with thick cover and mid-mountain grassland to c. 2500 m. In Australia apparently 2 main populations: one coastal in marshy heaths and swampy tussock grassland, other inland on floodplains, frequenting treeless tussock grassland and swampy depressions containing areas of rushes, sedges and lignum (*Muehlenbeckia*), also flooded bore drains. While normally perching only on ground, recent Australian observations included perching on tops of young pine trees.

Food and Feeding. Specialized rodent-hunter; in Australia, also small dasyurid marsupials (*Sminthopsis*, *Plaginale*); rarely, ground birds such as buttonquails (*Turnix*), reptiles, frogs, and large insects such as grasshoppers (Saltatoria), locusts (Acrididae) and cicadas (Cicadidae). Unlike *T. alba*, hunts entirely by low, quartering flight, with glides and hovers, similar to harriers (*Circus*), plunging head-first into grass. As with *T. capensis*, hunting begins earlier than *T. alba* and finishes later; in Australia, this pattern found in situations of stress after inland rodent plagues, when hunting began about 1 hour before dusk and continued to mid-morning. Although rarely seen unless flushed, in NE Australia plagues of e.g. long-haired rats (*Rattus villosissimus*) and cane rats (*R. sordidus*) may result in relatively large concentrations of this species, often mixed with *T. alba*, *T. novaehollandiae* and other raptors. When rat numbers crash, many owls starve.

Breeding. Oct-Mar, mostly Oct-Dec, in India, but once Jul; Sept-Jan in China and Philippines; May-Jun in Papua New Guinea; Feb-Sept in E coastal Australia; at any time of year depending on conditions in inland Australia. Usually solitary, but in favourable conditions sometimes loosely colonial, with nests separated by few hundred metres. Nest on ground in dense grass usually over 1 m high, or in sedges, usually away from trees, but in Australia once below mangrove and recently in young pine plantation; flimsy pad or mat of grasses soon trampled by nesting activity, canopied in grass and with series of (usually 3) approach tunnels or pathways, even over shallow water, made by pushing through to nest; entrance to main tunnel flattened by frequent food deliveries. Clutch 4-6 eggs in India, 3-8 in Australia, more pearl-shaped than in other *Tyto*, usually laid at 2-day intervals; incubation 31 days in Australia; natal down white, second (mesopile) down whitish in Philippines, buffy in China, tawny to buff or golden-brown in Australia; young fledge after c. 2 months, hiding in grass during day and returning to nest at night, and may stay around nesting area for some weeks, at least in Australia.

Movements. Generally sedentary throughout much of range, with some post-breeding dispersal of juveniles. Earlier reports of migration in China and Philippines subsequently attributed to winter breeding activities in former country and occasional flocking in latter. Records of vagrancy within Australia explained by general nomadism and dispersal of inland birds when favourable breeding conditions terminate, but such movements may also involve some coastal birds, particularly juveniles; N Australian populations possibly not permanent, but result of population explosions in interior; vagrancy elsewhere in Australia probably represents post-breeding dispersal of juveniles, usually coastward, including offshore islands, with nominate race recorded in SE & SW Australia, Palm Is and Magnetic I off Queensland, and Torres Strait islands. The few records from Indonesia, New Caledonia and Fiji (Viti Levu) may be of inland Australian birds, which are more likely to wander such distances; although it has been suggested that records from some of these islands indicate resident or former resident populations, it is not known if breeding has occurred on any of them. In E New Guinea normally found above 2500 m, but sometimes down to c. 400 m, and record of 2 birds from SE lowlands may represent vagrancy of nominate race from N Australia. Recent

observations of dark *Tyto* owls on several Fijian islands may have included present species, but unconfirmed, and probably *T. alba* although no dark morph of latter known there. Recorded (*chinensis*) as possible vagrant to Hong Kong, but probably captive escapes; also, May 1975 record from Iriomote, S Ryukyu Is, Japan, said to be *pithecopus* but could be *amaurona* (specimen lost). **Status and Conservation.** Not globally threatened. CITES II. Rare to very rare throughout most of range, but can be locally common in undisturbed areas or during rodent plagues (Australia). Strongholds appear to be India, Australia and New Guinea. In Indian subcontinent, described as rare and local or very local, and no recent records from Bangladesh. Much of apparent rarity possibly due to lack of observations or confusion with *T. alba*, but population declines caused by hunting and habitat loss likely, e.g. in China, Taiwan, Philippines and parts of coastal Australia. In NE Australia, rodenticides used since 1992 for rat control in cane fields have caused local population declines of 75-85%. Patchy distribution indicates possible recent fragmentation, e.g. nominate race and *chinensis* may have had continuous distribution in S Asia but now separated; it has been suggested that they may intergrade W of Vietnam, and also that nominate form probably occurred in Thailand until recently, but no suitable habitat remains there. Also, sufficient similarity between Indian and Australian birds has led to suggestion that the species would be found in Malaysia and W Indonesia, but no known records yet.

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Subfamily PHODILINAE

Genus *PHODILUS* I. Geoffroy Saint-Hilaire, 1830

15. Oriental Bay-owl

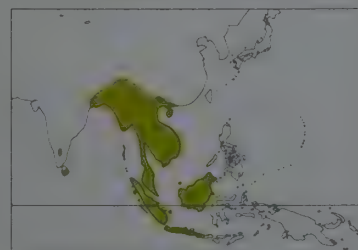
Phodilus badius

French: Phodile calong **German:** Maskeneule **Spanish:** Lechuza Cornuda
Other common names: Bay Owl, Asian Bay-owl; Sikkim Bay-owl (*saturatus*); Peninsular Bay-owl (*ripleyi*); Ceylon Bay-owl (*assimilis*)

Taxonomy. *Strix badia* Horsfield, 1821, Java. Relationships uncertain. Although has occasionally been considered to include *P. prigoginei* as a race, latter seems to exhibit much too marked differences. Taxonomic status of SE Asian forms requires clarification: birds of Thailand sometimes assigned to *saturatus* and sometimes to nominate *badius*, with those of Myanmar considered intermediate; present arrangement, with populations from N & C Myanmar E to Vietnam and China placed with Indian birds in *saturatus*, and those of S Myanmar and peninsular Thailand in nominate race, perhaps tentative, and extent of possible intergradation between the two in C? & S Myanmar and SW Thailand undetermined. Races *ripleyi* and *arixuthus* might be untenable, as based on unique types. Also, single record from E Philippines (Samar) described as separate race, *riverae*; included in nominate race in recent works, though size and colour characters in type description suggest closer affinities to *saturatus*, or possibly a valid race, but specimen destroyed in 1945 and no further conclusions possible. Six subspecies tentatively recognized.

Subspecies and Distribution.

P. b. saturatus Robinson, 1927 - Sikkim and NE India, N & C Myanmar and Thailand (except peninsular) E to Vietnam and SE China (S Yunnan, SW Guangxi Zhuang, Hainan I); presence in Nepal, Bhutan and Bangladesh unconfirmed.
P. b. ripleyi Hussain & Reza Khan, 1978 - Anaimalai-Nelliampathy Hills (SW India).
P. b. assimilis Hume, 1877 - C & S Sri Lanka.
P. b. badius (Horsfield, 1821) - Malay Peninsula and Greater Sundas (including Nias).
P. b. arixuthus Oberholser, 1932 - Natuna Is (Bungaran).
P. b. parvus Chasen, 1937 - Belitung I.



nominate but generally paler, with larger white spots above; *parvus* like nominate but smaller, with shorter bill and smaller feet; form '*riverae*' said to have chestnut, boldly streaked upperparts. Voice. Wide variety of calls. In breeding season, once described as surpassing all other owls in appalling nature of its cries, even sounding like half a dozen cats fighting; a single soft hoot; loud 3-note whistle

Descriptive notes. 23-33 cm; 255-308 g. Small, dainty owl with short ear-tufts projecting above sides of head. Chestnut-bay above, spotted with gold, wings barred black; facial disc rather square-shaped, pale greyish-pink; underparts light pinkish-buff, spotted black; eyes very large, blackish. Sexes alike. Juvenile presumably like adult. Races based mostly on variability of brown upperparts, black markings, barring on primaries and size: *assimilis* with dark brown speckled upperparts; *ripleyi* slightly larger, with chocolate-brown, finely stippled upperparts; *saturatus* larger than both, with chestnut, sparsely stippled upperparts; *arixuthus* like

like person calling dog, birds answering each other in forest; also described as a long, musical sequence, opening phrase of 3 notes, second higher than others, succeeded by 3 or 4 rising, quavering phrases, each beginning at successively lower point on scale, "hu-hli-hu, hu-u-u, hu-u-u..."; soft hoot and ringing "hooh-weeyoo"; different type of call depicted as "kwankwit-kwankwit-kek-kek-kek", given in flight in darkness; in captivity, also piercing wail and harsh scream, as well as chuckling sound when food offered, and loud whip-crack sound when frightened.

Habitat. Evergreen and mixed deciduous forest, landward edge of mangrove, partially cleared land and plantations, rarely straying outside these areas. Up to 2200 m; in NE India, foothills to 1500 m; in Sri Lanka, wet lowlands and lower hills. Day roost in hollow tree.

Food and Feeding. Small mammals, birds, lizards, snakes, frogs and large insects, particularly beetles; among avian prey, preference for flowerpeckers (*Dicaeum*) noted in Borneo. Hunts from perch, using rhythmic rocking of head to focus gaze, and captures prey in flight. Strictly nocturnal and usually hunts under forest canopy, where short, rounded wings well suited for rapid flight amid maze of small, vertical stems; with lack of horizontal branches, perches sideways on vertical saplings, behavioural trait once considered unique among owls but recorded also for *Tyto tenebriosa* and *T. multipunctata*.

Breeding. Nov in Sri Lanka, Mar-May in India; eggs laid Oct-Dec in Borneo. Nest an unlined hollow in tree trunk or rotten stump, c. 2-5 m up; same site used over many years, becoming heavily littered with pellets and other debris; one pair laid in nestbox in oil-palm plantation. Clutch 3-5 eggs; incubation and other details undescribed.

Movements. Presumably sedentary, with evidence of some movement, probably post-breeding dispersal of juveniles. Records of nominate race on Penang and Singapore, where species does not breed, indicate some over-sea dispersal; single record in E Philippines, on Samar in 1924, if not part of undiscovered (now extinct) breeding population, would represent surprisingly long-distance vagrancy.

Status and Conservation. Not globally threatened. CITES II. Considered very rare throughout range, though thought to be relatively common in S Malaysia, especially in lowland forest. No Bali record since 1911; extinct in Singapore since 1920's; single record from Nepal in 1846 of doubtful provenance; race *ripleyi* first discovered in SW India in Apr 1976, with only 3 subsequent records. Habits suggest that it can be easily overlooked; on other hand, is nearly helpless if found roosting in daylight, as observed with rediscovery of *ripleyi* in 1992. However, while perhaps genuinely rare in various parts of range, observations suggest adaptability to disturbed forest and other areas affected by human activity, and nesting sites have been found near buildings.

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16. Congo Bay-owl

Phodilus prigoginei

French: Phodile de Prigogine **German:** Kongomaskeneule **Spanish:** Lechuza del Congo
Other common names: African/Prigogine's/Tanzanian Bay-owl, Congo/Itombwe Owl

Taxonomy. *Phodilus Prigoginei* Schouteden, 1952, Muusi, 2432 m, Itombwe Mountains, Zaire. Occasionally treated as race of *P. badius*, but this seems hardly probable, and the two do not appear closely related; inclusion in *Phodilus* perhaps questionable; present species shows some similarities to *P. badius* in plumage coloration, but shape of facial disc rather different, more heart-shaped, as in *Tyto*. Monotypic.

Distribution. Itombwe (Mitumba) Massif, extreme E Zaire; also probably adjacent SW Rwanda (Nyungwe forest) and NW Burundi (near Teza).



Descriptive notes. Female c. 23-29 cm, 195 g. Male undescribed, presumably similar to female. Female deep rufous-brown above, feather tips with small black-edged white spots, wings and tail barred dark brown; facial disc light rufous-buff, with darker rim; pale rufous below, breast and flanks finely spotted dark brown; eyes relatively small, dark brown to blackish. Differs from *P. badius* in heart-shaped (not squarish) facial disc, lack of ear-tufts, more compressed bill and relatively small feet with robust claws. Juvenile unknown. Voice. Unconfirmed but probable Rwanda record based on call, described as "wok wok wok", considered structurally similar to that of *P. badius*.

Habitat. Both definite records from montane forest interspersed with bamboo thicket and grassland, at 1830 m and 2430 m; 1 bird discovered roosting in a grass clearing, subsequently recorded flying 50 m inside gallery montane forest (wooded valleys and scrubby open tops). Two probable records from similar habitats, at 2000 m and 2500 m. Presumably depends on forest, including selectively logged forest and edge; probable Burundi sighting, in forest surrounding tea estate, suggests possible use of hunting territory outside forest.

Food and Feeding. Undescribed.

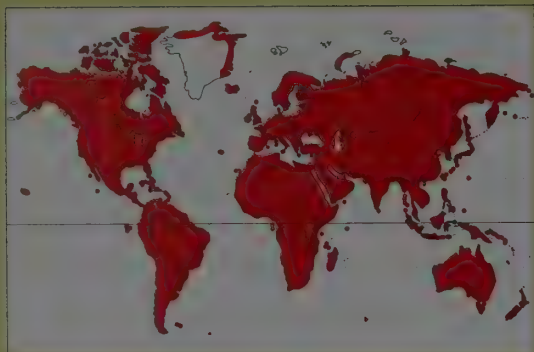
Breeding. Undescribed.

Movements. Presumably sedentary.

Status and Conservation. **VULNERABLE.** CITES II. Restricted-range species; present in Albertine Rift Mountains EBA. Rare and elusive. Many unsuccessful attempts to find the species since its initial discovery in Mar 1951, until rediscovered (mist-netted and released unharmed) in same region in May 1996. The two unconfirmed records are very close to species' only known locality, the nearest being c. 50 km to E, where probably heard in Jan-Feb 1990; Burundi observation, however, was as long ago as Dec 1974. Further research clearly required.

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Class AVES
Order STRIGIFORMES
Family STRIGIDAE (TYPICAL OWLS)



- Large-headed nocturnal birds with strong, hooked bill, round facial disc, compact body, moderately short tail, and strong feet with sharp talons; plumage soft and cryptically coloured.
- 12-75 cm.



- Cosmopolitan.
- Virtually all terrestrial habitats, from Arctic to tropics; typically found from sea-level to c. 2000 m, but locally up to 4700 m.
- 25 genera, 189 species, 548 taxa.
- 21 species threatened; probably 1 of these, as well as 4 other species and 2 subspecies, extinct since 1600.

Systematics

With some 189 living species, Strigidae is by far the larger of the two families that form the order Strigiformes. Ranging in size from the diminutive Elf Owl (*Micrathene whitneyi*) at 40 g to the immense Eurasian Eagle-owl (*Bubo bubo*) at 4 kg or more, the typical owls nonetheless comprise a distinct and easily recognized group of predatory birds. Within the family, however, similarities in plumage and morphology, coupled with a basic lack of information on the behaviour of many species, have led to considerable confusion regarding species and even generic limits. Indeed, the internal taxonomy of the Strigidae may be in a greater state of turmoil than is that of any other family of non-passerine birds. The problem is especially acute in *Otus* (scops-owls and screech-owls) and *Glaucidium* (pygmy-owls and owlets) that inhabit tropical forest, in which fieldwork is notoriously difficult. Recent studies based largely on analyses of vocalizations have revealed that the numbers of species within these genera have been greatly underestimated. Without question, many species remain to be described: some that await discovery in the wild, and others that have been misclassified because nothing is known of their biology. Truly, these are exciting times for the owl taxonomist.

Owls are well represented in the fossil record. As paleontologist S. L. Olson has pointed out, however, our understanding of their evolutionary history is incomplete, owing to the lack of a comprehensive revision of the fossil taxa. The oldest fossils attributed to owls were fragments of leg bones discovered in Upper Cretaceous deposits in Romania. Described as two species in a new fossil family Bradynemidae, these fossils were in fact from small dinosaurs. The oldest known fossil that unquestionably is an owl, *Ogygopteryx wetmorei*, was discovered in Colorado, USA, in Paleocene deposits that are about 58 million years old. The description of this form was based on a nearly complete tarsometatarsus, and the species was placed in the extinct family Ogygopterygidae.

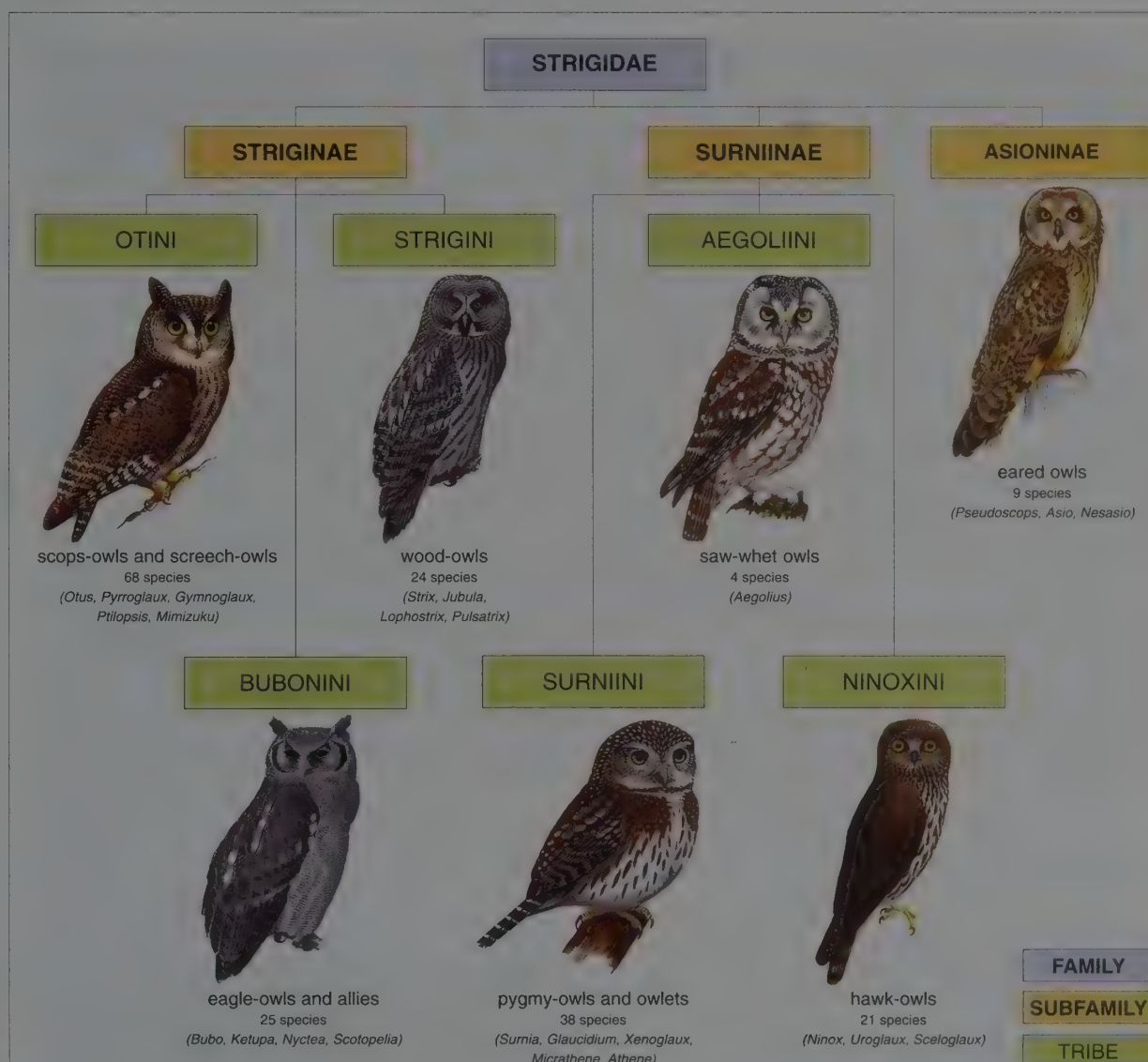
Owls are believed to have undergone a major radiation in the Eocene or late Paleocene, more than 50 million years ago. Three extinct families of owls have been described from middle and late Eocene deposits in western North America and from late Eocene to early Oligocene deposits in the Phosphorites du Quercy, France. The Quercy fossils also show that the family Tytonidae, which includes the modern barn-owls, was highly diversified in Europe during the Eocene (see page 34). The ex-

act timing of the appearance of the family Strigidae is uncertain. Seven species from Quercy that were originally placed in the Strigidae (including a "*Bubo*" and an "*Asio*") actually belong to the Tytonidae. *Bubo poirrieri* from the Lower Miocene of France approximately 24 to 22 million years ago, and *Strix brevis* from the Lower Miocene of western North America, are among the earliest fossils reliably attributed to the Strigidae. Thus, it appears that the Tytonidae preceded the Strigidae during the evolutionary history of owls, and that Strigidae is of Neogene origin.

Some of the relatively recent fossil owls are especially interesting, because their remains suggest that they were vastly different from the owls of today. For instance, *Ornimegalonyx oteroi* from the Pleistocene of Cuba was absolutely gigantic: its height exceeded 1 m, its tarsus was twice as long as that of the Eurasian Eagle-owl, and it had the most powerful claws of any known owl. *Ornimegalonyx* was closely related to *Strix*. As stated by O. Arredondo, who described this giant in 1976, "*Ornimegalonyx* had to have been the scourge and terror of most of the larger mammals of the Pleistocene of Cuba."

Also deserving of mention is a distinctive group of owls that was endemic to the Hawaiian Islands. In 1991, S. L. Olson and H. F. James described four species in the genus *Grallistrix* (literally, "stilt owl" in reference to the long legs), one each from the islands of Kauai, Oahu, Molokai and Maui. Of Holocene origin and derived from *Strix*, these owls, along with dozens of other species of extinct birds, would perhaps be alive today were it not for the colonization of the Hawaiian Archipelago by humans approximately 1600 years ago. The long legs and shortened wings of *Grallistrix* were probably adaptations for catching birds, and in this manner *Grallistrix* would have been convergent with the bird-eating hawks of the genus *Accipiter*. That species of *Grallistrix* specialized on avian prey is not unduly speculative. Fossil owl pellets discovered by Olson and James contained the remains of various species of passerines; also, the terrestrial vertebrate fauna of Hawaii prior to the arrival of humans was devoid of rodents and other small mammals.

The order Strigiformes comprises a well-defined group of predatory birds with a strong, hooked bill; a cere at the base of the bill; and sharp, strongly hooked talons. These features are also characteristic of the diurnal birds of prey. In 1758, this convergence in trophic appendages led Linnaeus to place the hawks and owls in the same group, the Accipitres, a practice that was followed, albeit with various name changes, by nearly every avian



Subdivision of the
Strigidae

[Figure: Ian Willis,
Tim Worfolk, Clive Byers,
Hilary Burn, Norman Arlott
& Ian Lewington]

taxonomist for the next 130 years. Around 1890, M. Fürbringer and H. von Gadow, among others, noted that owls shared many characters with the nightjars and concluded that the closest relatives of the owls would be found within the suborder Caprimulgi. From that time onwards, the notion that owls were related to nightjars gained nearly universal acceptance, with one notable exception. In 1981, J. Cracraft revived the idea that owls and falconiforms were closely related, this being based on what he perceived to be shared derived characters of the pelvis and the tarsometatarsus. This non-conformist view has not been well received by other ornithologists, most of whom would place the nocturnal and diurnal birds of prey in separate orders.

On the basis of DNA-DNA hybridization data, C. G. Sibley and J. E. Ahlquist placed owls and nightjars in separate suborders within the Strigiformes. Sibley and Ahlquist's data clearly indicate that owls and hawks are not closely related and suggest that turacos (Musophagidae) are the closest living relatives of owls and nightjars. Analysis of mitochondrial DNA by N. Kuroda and associates also supports a relationship between owls and nightjars. The genetic evidence for a close relationship between owls and nightjars is perfectly acceptable, but it seems more appropriate in the present work to follow traditional usage in recognizing the nightjars to be placed in their own order, Caprimulgiformes, juxtaposed to Strigiformes, which thus contains only the very closely related families Tytonidae and Strigidae. Despite the obvious links between these two families, certain well-marked differences clearly support their segregation into two families (see Morphological Aspects).

As for the internal organization of Strigidae itself, J. L. Peters used characters of the external ear and facial disc to divide it into the subfamilies Buboninae, containing 21 genera, and Striginae, with six genera. Bubonine owls have relatively small external ears, no ear flaps, and a facial disc that is more extensive below the eyes than above. In contrast, strigine owls have large ear openings with fleshy flaps, a ligamentous bridge across the opening, and a well-developed facial disc that is just as extensive above the eyes as below. L. H. Kelso and K. H. Voous questioned whether characters of the external ear were taxonomically useful, given their findings that ear size and shape were not completely diagnostic for the two subfamilies. In addition, N. L. Ford pointed out that generic limits in the typical owls were based solely on external morphology such as bill shape and characters of the nostril and cere. Ford's comparative analysis of osteology among owls led to a very different classification from that of Peters.

Ford discovered that the postcranial bones of the strigids gave little clue as to relationships at the subfamily level. The characters of the skull were informative, however, and Ford concluded that the family Strigidae consisted of three distinct groups, which he proposed as the subfamilies: Striginae, containing three tribes and 13 genera; Surniinae, with three tribes and eight genera; and Asioninae, consisting of just two genera. Ford's classification has not been widely adopted by ornithologists, in part because of the highly divergent classifications proposed for owls, and perhaps because it was never published in the open literature. However, the recent work of Olson and James is in general agreement



Placed together in the order Strigiformes, the "true owls" of the family Strigidae and the barn-owls in the Tytonidae are clearly closely related. Both groups are characterized by a strong, hooked bill with a cere at the base, and strongly hooked, sharp talons. Strigid owls differ most obviously from tytonids, however, in having a rounded facial disc rather than the classic heart-shaped disc of the barn-owls. Further differences include the more rounded skull with relatively larger orbits, a furcula that is not fused to the sternum, and a naked uropygial gland, while the strigid sternum has four notches rather than two.

[*Bubo bubo bubo*, Germany.
Photo: Dietmar Nill/
BBC Natural History Unit]

with Ford's conclusions, and most of Ford's classification has been adopted here. Incorporating recent changes in thinking on generic limits, altogether 25 genera of strigids are recognized, arranged into the three subfamilies.

Little can be said about subfamilies in the Strigidae based on DNA-DNA hybridization because Sibley and Ahlquist lacked DNA samples for most of the genera. A study of allozyme divergence in six species of owls, namely the Eurasian Scops-owl (*Otus scops*), Eurasian Eagle-owl, Tawny Owl (*Strix aluco*), Little Owl (*Athene noctua*), Northern Long-eared Owl (*Asio otus*) and Short-eared Owl (*Asio flammeus*), was undertaken by E. Randi and associates; the results suggested that *Athene* was ancestral to modern Strigidae. More recently, M. Wink and P. Heidrich examined nucleotide sequences in the cytochrome-*b* gene of 13 genera of Strigidae. By and large, their results corroborated many of Ford's conclusions that were based on cranial osteology. A clearer understanding of the phylogenetic placement of taxa within the Strigidae will not be possible until genetic analyses are conducted on a larger sample of genera and species.

The tribe Otini contains the widespread genus *Otus*, the monotypic *Pyrroglau*x and *Gymnoglaux*, the two African *Ptilopsis*, and the Philippine *Mimizuku*. *Otus*, comprising the scops-owls and screech-owls, is by far the most diverse owl genus in terms of species, with some 63 inhabiting all continents except Antarctica and Australasia, although it just creeps into the latter off northern New Guinea, where the Biak Scops-owl (*Otus beccarii*) is found. Most of the species occur in Asia, including the islands of Indonesia, and in the New World tropics. The typical Old World scops-owls, placed in the subgenus *Otus* by J. T. Marshall and B. F. King, tend to have short, simple songs. In contrast, the New World screech-owls in the subgenus *Megascops* have long, complex songs that often contain fast trills. On the basis of its slow, simple song, the Flammulated Owl (*Otus flammeolus*) of the pine forests of western North America is placed with the scops-owls, being the only New World member of that subgenus.

Most members of the tribe Otini are small to medium-sized and have short legs, conspicuous ear-tufts, and cryptic plumage with much streaking and barring. An exception to this general pattern is the Cuban Screech-owl (*Gymnoglaux lawrencii*), which has no ear-tufts and has long legs resembling those of the Bur-

rowing Owl (*Athene cunicularia*); another is the Palau Owl (*Pyrroglau*x *podarginus*), which is also virtually tuftless, has relatively long legs, and has black-and-white tail-coverts and a white carpal patch, in marked contrast to other members of the tribe. Both of these species are sometimes placed in *Otus*, and both occur on islands where no other species of Otini exist, suggest-



One of a number of monotypic genera in the Strigidae is *Uroglau*x, the Papuan Hawk-owl. This is thought to be closely related to the hawk-owls of the genus *Ninox*, and is sometimes included with the latter. It is strikingly similar to some *Ninox*, in particular the Rufous Owl (*Ninox rufa*), in having strongly barred upperparts and tail, but it differs from that species in having streaked, rather than barred, underparts.

[*Uroglau*x *dimorpha*, Goldie River, Papua New Guinea.
Photo: Eric Lindgren/
Ardea]



Another monotypic genus contains the Crested Owl, a very strange-looking owl restricted to forest areas from south-east Mexico to Brazil. In terms of its external appearance, this species would seem to have no really close relatives. It bears a superficial resemblance to *Jubula*, and the two genera have sometimes been merged, but the similarities between the two may be due simply to convergence. Some studies have claimed to show both to be linked with *Otus* and with *Bubo*, and an apparent similarity to *Otus* in cranial characters was demonstrated in one case.

More recent work has indicated a possible connection between *Lophotrix* and *Pulsatrix*, based on similarities in postcranial skeleton and in the juvenile plumages of the two. It seems that only further research will reveal the true affinities of the intriguing and little-known Crested Owl.

[*Lophotrix cristata stricklandi*,
La Selva Biological

Station, Costa Rica.

Photo: José Luis Rangel Salazar]



Four Strix owls inhabiting humid forest in the Neotropics, including the aptly named Black-and-white Owl, were formerly placed in the genus *Ciccaba*, it being considered that they differed from other Strix species in the size of their external ears and their dermal flaps. On the other side of the Atlantic, a single species, the African Wood-owl (*Strix woodfordii*), appeared to show the same structure and was therefore also placed in *Ciccaba*. Later work, however, has revealed no osteological difference between the two groups, which are now merged, this treatment being supported also by DNA studies.

[*Strix nigrolineata*, Costa Rica.
Photo: Michael & Patricia Fogden]

ing that their morphological adaptations were reinforced in an environment devoid of close competitors.

Similarities in appearance have made classification of some species of *Otus* difficult. For example, the Western (*Otus kennicottii*) and Eastern Screech-owls (*Otus asio*), with largely non-overlapping ranges encompassing most of the USA, were classified as a single species until 1983, when the significance of subtle differences in their plumages and vast differences in their vocalizations, in conjunction with new perceptions in species concepts, led to their classification as allospecies within a superspecies complex. Going in the other direction, an undescribed taxon from the arid woodland of north-western Peru was thought to be a new species until N. K. Johnson and R. E. Jones conducted an in-depth analysis of its vocalizations. Despite significant differences in size, the new taxon proved to be more appropriately treated as a subspecies of the Peruvian Screech-owl (*Otus roboratus*) and was described as *O. r. pacificus*.

Species limits in *Otus* are especially sticky in Asia, where the presence of many distinct and little-known populations has yielded several taxonomic nightmares. The "Collared" scops-owl group is a case in point. In 1940, Peters listed 18 subspecies of *Otus bakkamoena* that ranged from India and Pakistan to South-east Asia, Japan and the Philippines. By 1978, J. T. Marshall recognized 13 subspecies of *O. bakkamoena* and considered one, the Mentawai Scops-owl (*Otus mentawi*), to be a full species. Subsequent work has led to the elevation of four more of Peters's races to full species status, so that his original single species now comprises the Mentawai, Indian (*Otus bakkamoena*), Collared (*Otus lettia*), Sunda (*Otus lempiji*), Japanese (*Otus semitorques*) and Palawan Scops-owls (*Otus fuliginosus*). A score or so of subspecies are divided among these six species. Furthermore, at the south-east edge of the range occupied by this group a seventh owl is found, the Philippine Scops-owl (*Otus megalotis*); although more often considered a full species, this, too, has sometimes been included within *Otus bakkamoena*. All seven species would seem best regarded as forming a superspecies.

Otus has also been a challenging group in South America, where a series of expeditions to remote cloudforest habitats has yielded several new species. In 1981, J. S. Weske and J. W. Terborgh described the Cloudforest Screech-owl (*Otus marshalli*) from the Andes of central Peru, and five years later, in 1986, J.

W. Fitzpatrick and J. P. O'Neill described the Cinnamon Screech-owl (*Otus petersoni*) from the Andes of northern Peru and southern Ecuador. In addition, Fitzpatrick and O'Neill proposed that the Colombian Screech-owl (*Otus colombianus*) of cloudforest on the west slope of the northern Andes was also specifically distinct, being closely related to the Rufescent Screech-owl (*Otus ingens*) of the eastern slope. All four species belong to a group of dark-eyed, as opposed to yellow-eyed, Neotropical screech-owls that also includes the amber-eyed Tawny-bellied Screech-owl (*Otus watsonii*) from lowland forest in the Guianas and Amazonia. The Cinnamon and Colombian Screech-owls are extremely similar in the colour and pattern of their plumage but differ in gross measurements, the Colombian being decidedly larger, and in their tarsi, which are large and nearly naked in the Colombian and smaller and partly feathered in the Cinnamon. Also, their voices differ notably, and it is in this respect that it is clear that the Colombian really belongs very close to the Rufescent Screech-owl; indeed, the two are nowadays often considered conspecific. It has been suggested that the Cinnamon Screech-owl may be conspecific with the Cloudforest Screech-owl, but the data available at present seem decidedly scant for such a conclusion. Further complications have emerged with these forms in the proposal that the Cinnamon Screech-owl might be conspecific with the type of "*Otus huberi*". Although this suggestion could be right, the type specimen of "*huberi*", collected more than a century ago, is in very poor condition and, having been mounted at one stage, it is difficult to ascertain the true extent of feathering on the tarsus. Given the circumstances, it would seem that there is little to be gained by resurrecting a long-forgotten name based on a damaged type specimen. A final uncertainty worth mentioning within this group refers to the southern race *usta* of the Tawny-bellied Screech-owl: this form may constitute a further full species, but at present the available data seem insufficient to justify such a split.

In 1966, a scops-owl collected on Great Nicobar Island in the Indian Ocean was erroneously considered a subspecies of the Oriental Scops-owl (*Otus sunia*). A second specimen was obtained in 1977, after which time Marshall treated it as an unnamed taxon of the Moluccan Scops-owl (*Otus magicus*). Two decades later, a re-examination of these specimens led P. C. Rasmussen, in 1998, to describe a new species, the Nicobar Scops-

Some modern taxonomists prefer to "lump" the Asian fish-owls with the eagle-owls in the genus *Bubo*. While the two groups are without doubt closely related, both morphologically and genetically, and also share certain vocal characteristics, there are decided differences between them. The fish-owls, the Buffy Fish-owl being a good example, have a far less pronounced facial disc and, importantly, have unfeathered tarsi and toes and have spiny scales on the soles of their feet. Whether these differences, which are related to the aquatic feeding ecology of the fish-owls, are sufficient for them to be separated generically, however, is a matter of dispute.

[Ketupa ketupu ketupu,
Danum valley,
Sabah, Borneo.
Photo: Günter Ziesler]



owl (*Otus alius*). The species is of uncertain taxonomic affinity but is morphologically closest to the highly variable superspecies complex that includes the Sulawesi Scops-owl (*Otus manadensis*). It has been suggested that it might form a superspecies with two owls from nearby Sumatran islands, the Simeulue (*Otus umbra*) and Enggano Scops-owls (*Otus enganensis*).

Two other newly described species from the Old World are the Sangihe Scops-owl (*Otus collari*) from Sangihe Island, north-east of Sulawesi, and the Moheli Scops-owl (*Otus moheliensis*) from the island of that name in the Comoros. In addition, Madagascar Scops-owls (*Otus rutilus*) from the humid eastern slopes of the island sing a series of 5-15 clear hoots, whereas those from the more arid west give a slower series of 3-7 notes that are less pure than those of the eastern birds. The two forms also differ subtly in morphology, and they probably represent different species. Again, the form of scops-owl from the Comoran island of Mayotte (Maore), currently classified as *O. rutilus mayottensis*, may be another that merits full species status, because it appears to differ vocally, as well as in size and perhaps some plumage characters. Other forms possibly awaiting discovery include one species from the Mascarene island of Reunion, and it has been claimed that the island of Sumba, in the Lesser Sundas, may harbour its own species of *Otus*, although, somewhat surprisingly, some sources put the reports down to misidentifications of the relatively large endemic Sumba Boobook (*Ninox rudolfi*)! Several of the forms in Indonesia currently listed as races seem likely to be promoted to full species over the coming years, particularly some that are currently attributed to the Moluccan and Sulawesi Scops-owls. Prime of these must be the form *sulaensis* of the Sula Islands, already proposed as a species by some authorities, and with a highly distinctive voice. Other firm candidates include *mendeni* of the Banggai Islands, *kalidupae* from the Tukangbesi Islands, and *siaoensis* of the island of Siau, between northern Sulawesi and Sangihe; admittedly, most of these forms remain known only from a handful of specimens, so much work remains in order to establish their status in terms of both taxonomy and conservation. Over the next few years it seems quite likely that the situation in the Comoros will thus progress to a remarkable four species being recognized within this very small archipelago. Even more spectacular, however, could be

the number of species that end up being recognized for the Sulawesi region.

Our understanding of species limits in *Otus* has progressed rapidly during the past 25 years, as witnessed by the fact that, in 1973, J. A. Burton recognized only about half the number of species that are accepted today. Despite this progress, however, it is clear that much remains to be learned. Given the complex nature of variation among the insular scops-owls from Indonesia and the cloudforest screech-owls of the Andes, future studies based on analyses of nucleotide sequences and vocalizations will undoubtedly expand considerably the number of species in this difficult group.

Still within the Otini, the white-faced owls inhabit scrubland and savanna throughout sub-Saharan Africa. The Northern White-faced Owl (*Ptilopsis leucotis*) gives a slow song not unlike that of an Old World scops-owl, whereas the Southern White-faced Owl (*Ptilopsis granti*) has a rapid song that has been compared to that of the Tropical Screech-owl (*Otus choliba*) from South America. Until quite recently, the two white-faced owls were considered to be conspecific and, moreover, were placed in the genus *Otus*. Analysis of the cytochrome-*b* gene, however, indicated that two species were involved, which makes perfect sense given the differences in their vocalizations. Furthermore, and surprisingly, this analysis also suggested that *Ptilopsis* is a sister taxon to the genus *Asio*. Although this potential relationship is recognized, for the present purposes *Ptilopsis* is retained within the subfamily Striginae.

The phylogenetic placement of the Giant Scops-owl (*Mimizuku gurneyi*), which is endemic to the Philippines, has been in question until recently. Attaining a length of 30 cm, *Mimizuku* has been considered an oversized scops-owl by some authorities and a stunted eagle-owl by others. Its song is described as a loud, single note that is unlike those of scops-owls or eagle-owls. Analysis of mitochondrial DNA by H. C. Miranda and associates has shown that *Mimizuku* is closely allied to *Otus* rather than to *Bubo*. The genetic similarities between *Mimizuku* and *Otus* are supported by similarities in cranial morphology, but differences between the two taxa in size, plumage and vocalizations suggest that phenotypic differentiation in *Mimizuku* has progressed more rapidly than has genetic differentiation.



The tribe Bubonini consists of the large and powerful eagle-owls (*Bubo*), fish-owls (*Ketupa*), fishing-owls (*Scotopelia*) and the Snowy Owl (*Nyctea scandiaca*). The eagle-owls are of Old World origin, 16 of the 18 species occurring in Asia or Africa, and only two, the widespread and polytypic Great Horned Owl (*Bubo virginianus*) and the monotypic Magellanic Horned Owl (*Bubo magellanicus*), inhabiting the New World. The last-named, although described as a species as early as 1828, has long been considered a race of the Great Horned Owl. Differences in voice, morphology and DNA, however, indicate that it is a separate species. The Rock Eagle-owl (*Bubo bengalensis*) of India and the Pharaoh Eagle-owl (*Bubo ascalaphus*) of North Africa have been treated as subspecies of the Eurasian Eagle-owl by many authorities; D. Amadon and J. Bull, however, considered all three to represent a superspecies complex, a conclusion that is also supported by recent analysis of the cytochrome-*b* gene. In addition, the Greyish Eagle-owl (*Bubo cinerascens*) of Africa seems better treated as a distinct species. Until recently considered a northern and western race of the Spotted Eagle-owl (*Bubo africanus*), it differs importantly from that species in having dark brown instead of yellow irides, as well as showing other less marked differences in plumage and size.

Eagle-owls and fish-owls are morphologically and genetically similar and are almost certainly close relatives; sometimes both groups are placed in *Bubo*. However, fish-owls differ from eagle-owls in having unfeathered toes and tarsi, spine-like scales on the soles of their feet, and a poorly developed facial disc. Each of these differences can be linked to the fact that *Ketupa* species feed almost exclusively on fish and other aquatic organisms. Blakiston's Eagle-owl (*Bubo blakistoni*) of eastern Asia was long considered to be a *Ketupa*, but it is extremely similar to the Eurasian Eagle-owl osteologically, and also has feathered tarsi.

The three species of *Ketupa* occur in tropical latitudes in Asia. The Tawny Fish-owl (*Ketupa flavipes*) and the Buffy Fish-owl (*Ketupa ketupu*) have relatively restricted adjoining ranges in and near South-east Asia, and are very closely related. The Brown Fish-owl (*Ketupa zeylonensis*) has a wider distribution that encompasses parts of the ranges of the other two species.

The fishing-owls are confined to Africa, where they seem to function as ecological equivalents of the Asian fish-owls. *Scotopelia* shares with *Ketupa* the unfeathered tarsi, spiny scales on the feet, and the poorly developed facial disc; it differs from *Ketupa* in lacking ear-tufts and in possessing loose feathering that gives the head a shaggy appearance.

The final member of the Bubonini, the Snowy Owl, is so distinctive in plumage and behaviour that it is placed in the monotypic genus *Nyctea*. The breeding range of this huge white owl is restricted to Arctic tundra in the Holarctic region. Despite obvious differences in outward appearance, *Nyctea* is very similar to *Bubo* osteologically and genetically, and might perhaps be placed between *Bubo* and *Ketupa* in recognition of this similarity. *Nyctea* differs from *Bubo* in having exceptionally dense plumage, an obvious adaptation to cold temperatures, and in exhibiting sexual dichromatism in which the female is more heavily pigmented than the male.

The tribe Strigini contains the wood-owls (*Strix*, *Pulsatrix*), the Maned Owl (*Jubula lettii*), and the Crested Owl (*Lophostrix cristata*). An additional genus, *Ciccaba*, was separated from *Strix* by Peters on the basis of the size of the external ears and their dermal flaps, but subsequent work by K. H. Voous showed that these genera could not be reliably separated by ear characters. N. L. Ford found no osteological characters that distinguished the two genera and recommended that they be merged, a conclusion also supported by DNA-DNA hybridization data.

The 19 species of *Strix* are relatively large owls that occupy a variety of forested habitats. They are absent from Australasia, whereas ten species are restricted to the New World and eight to the Old World, and one, the Great Grey Owl (*Strix nebulosa*), is Holarctic. Four of the five *Strix* that have traditionally been placed in *Ciccaba* inhabit humid forest in the Neotropics: these are the Mottled (*Strix virgata*), Black-and-white (*Strix nigrolineata*), Black-banded (*Strix huhula*) and Rufous-banded Owls (*Strix albitarsis*). The fifth, the African Wood-owl (*Strix woodfordii*), is the sole member of *Strix* that occurs in the Afrotropical region.

The widespread Tawny Owl of Eurasia and the uncommon Hume's Owl (*Strix butleri*) of the Middle East have been considered conspecific by some authorities. However, studies of

The taxonomy of the Striped Owl has been argued over for some years. Originally placed in a monotypic genus Rhinoptynx, it was later placed in Asio on the basis of similarities in cranial characters. Subsequent work, however, appeared to identify subtle differences between the two in these same characters of cranial morphology, and it was then suggested that Rhinoptynx should really be merged with Pseudoscops, both being equally primitive forms.

[*Asio clamator clamator*, Minas Gerais, Brazil. Photo: Luiz Claudio Marigo]



*In tandem with debate over the taxonomic validity of Rhinoptynx, an unpublished analysis of a specimen of the Stygian Owl found that bird, too, to be closely allied to Pseudoscops. With the advantage of modern methods of molecular-biological analysis, however, it has recently been shown that both the Striped Owl (*Asio clamator*) and the Stygian Owl do in fact belong with other *Asio* species. Thus, the Jamaican Owl remains the sole member of the genus *Pseudoscops*.*

[*Asio stygius stygius*, Araçuaí, Minas Gerais, Brazil. Photo: Edson Endrigo]

The Strigidae family contains many examples of taxa which pose problems in terms of their classification. A good case is presented by the African Long-eared Owl. This bird has often been considered a subspecies of the Northern Long-eared Owl (*Asio otus*), but it is larger and darker than that species, and its chequered underparts, as well as its more powerful feet and bill and its vocal characters, appear sufficiently different that it is now generally regarded as a full species.

[*Asio abyssinicus abyssinicus*,
Bale Mountains, Ethiopia.
Photo: Göran Ekström]

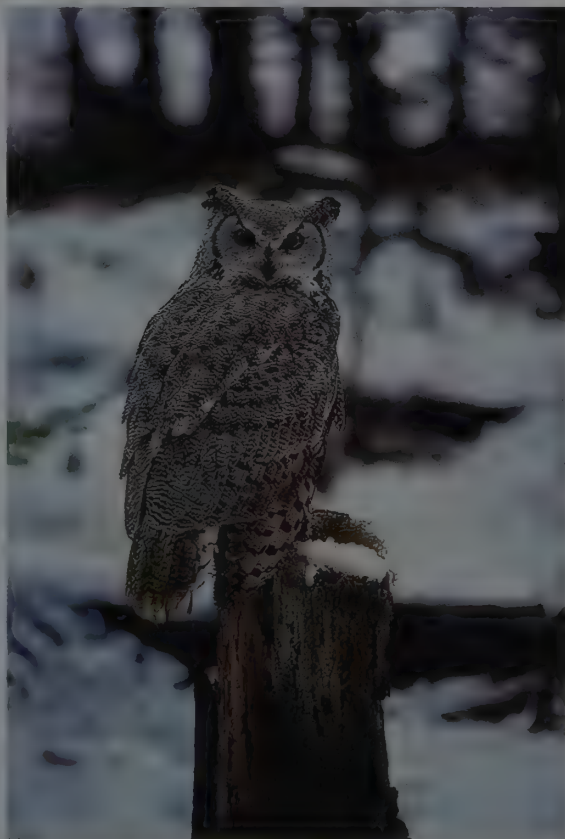
When considering whether a subspecies is sufficiently distinct to have reached the level at which it may be treated as a full, separate species, it is important to determine to what extent, if any, it intergrades with other populations of the species in question. The large and pale northern race of the Great Horned Owl would appear distinctive enough, but the situation is complicated by the fact that intergrading populations occur at the boundaries between races. Even the validity of some subspecies is controversial.

[*Bubo virginianus subarcticus*,
northern British Columbia,
Canada.
Photo: Kenneth Fink/Ardea]

nucleotide sequences in the cytochrome-*b* gene by Heidrich and Wink indicate that Hume's Owl is a valid species and suggest that it is actually more closely related to the African Wood-owl than to the Tawny Owl. Further, the work of R. Straneck has demonstrated that the northern population of the Rufous-legged Owl (*Strix rufipes*) is a distinct species, the Chaco Owl (*Strix chacoensis*), which differs from southern birds in its vocalizations and its plumage colour; together, these two form a superspecies that occurs throughout much of southern South America. Although perhaps of no taxonomic significance, an interesting situation has occurred in western North America, where the widespread Barred Owl (*Strix varia*) has recently colonized the more restricted range of the Spotted Owl (*Strix occidentalis*). Between 1989 and 1992, four hybrids were recorded in Oregon and Washington, USA, raising the question of whether the expanding Barred Owl population is having a detrimental effect on the threatened Spotted Owl (see Status and Conservation).

In the tropical rainforest of Central and South America, the three *Pulsatrix* species form a group of large, striking owls, all having a dark face with contrasting light "spectacles" that give the birds a scowling appearance. Formerly thought to be allied with *Bubo*, *Pulsatrix* is clearly closer to *Strix* in its osteology. The widespread and fairly common Spectacled Owl (*Pulsatrix perspicillata*) occurs from southern Mexico to Argentina and consists of six subspecies. In contrast, the rare and little-known Band-bellied Owl (*Pulsatrix melanota*) and Tawny-browed Owl (*Pulsatrix koeniswaldiana*) occupy restricted and non-overlapping ranges in western and eastern South America, respectively.

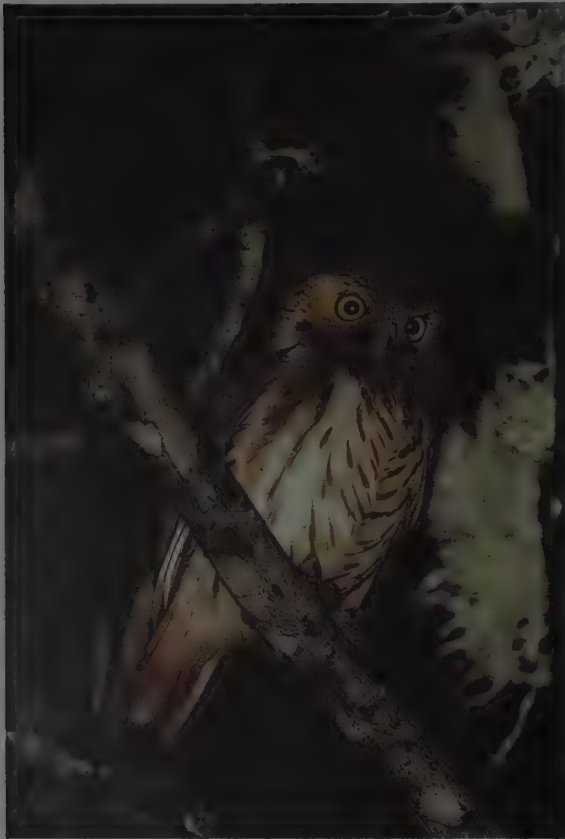
Almost nothing is known about the biology of the two species in the monospecific genera *Lophotrix* and *Jubula*, and their taxonomic affinities are unclear as well. They have been linked with *Otus* and *Bubo*, and some authorities merge the two genera, recognizing only *Lophotrix*. Ford placed them in the tribe Otini on the basis that they shared cranial characters with *Otus*. Subsequent work by R. W. Storer indicated that *Lophotrix* was closer to *Pulsatrix*, the two showing similarities in the postcranial skeleton and in the juvenile plumage. Following Storer, the present treatment places *Lophotrix*, and by extension *Jubula*, in the tribe Strigini.



Surniini is the largest of the three tribes in Surniinae and includes *Glaucidium*, the second most numerous genus of owl. Three of the five genera are monospecific. The Northern Hawk-owl (*Surnia ulula*) is a long-tailed, medium-sized inhabitant of boreal forest in the Old and the New Worlds. Genetic analysis indicates that *Surnia* shares a common ancestor with *Glaucidium*. The Long-whiskered Owlet (*Xenoglaux loweryi*) is known from only five specimens collected on the east slope of the Andes in Peru. The fan-like extension of its facial ruff is unique among owls. Very little is known about this peculiar little owl (indeed, *Xenoglaux* translates as "strange owl") other than that it appears to be closest to *Micrathene* and *Glaucidium*. The Elf Owl is the world's smallest owl and the sole member of the genus *Micrathene*. It occupies deserts and open woodland in the southwestern USA and northern Mexico. *Micrathene* shares cranial characters with *Glaucidium* and *Athene*, but it is unclear which genus is the closer relative.

The 31 species of *Glaucidium* are small diurnal or crepuscular owls that prey on insects, reptiles and small birds. They can be conveniently divided into two groups: the pygmy-owls of the New World and temperate Eurasia, with 19 species and one species, respectively; and the eleven owlets of Africa and tropical to subtropical Asia, six of which inhabit the former and five the latter. Classification of *Glaucidium* is complicated by the fact that some taxa exhibit intraspecific plumage dichromatism, some are very similar in plumage and morphology, and many are unstudied in the wild. Consequently, the taxonomy within the group is in greater flux than is that of any other genus of owl. The rapid progress in our understanding of the genus is reflected by the fact that, as recently as in 1988, Amadon and Bull recognized only 15 species of *Glaucidium*. Recent work on vocalizations and genetics, especially in the New World tropics, has more than doubled that number.

C. König's 1991 monograph on pygmy-owls of the South American Andes was the first comprehensive treatment of multiple species of *Glaucidium* based on vocalizations. König classified the taxa into three groups: species uttering long series of single, equally spaced notes; those uttering trills and single notes, or trills only; and species uttering note sequences mainly in cou-



plets. The first group was represented by the Ferruginous (*Glaucidium brasilianum*), Peruvian (*Glaucidium peruanum*) and Austral Pygmy-owls (*Glaucidium nanum*); the second by the Andean (*Glaucidium jardinii*), Yungas (*Glaucidium bolivianum*) and Amazonian Pygmy-owls (*Glaucidium hardyi*); whereas series of couplets were given by the Least Pygmy-owl (*Glaucidium minutissimum*). Two of these species, the Yungas and the Peruvian, were new to science, and one, the Austral Pygmy-owl, was elevated from a subspecies of the Ferruginous Pygmy-owl. More recent work on the Ferruginous Pygmy-owl complex suggests that the two taxa *ridgwayi* and *cactorum* from Central America, Mexico and the south-western USA, currently treated as subspecies of the Ferruginous, probably constitute a separate species. Until further details are available, however, it is probably better to consider the Ferruginous Pygmy-owl to be a very widespread species consisting of some nine races. Again, J. Fjeldså and G. Engblom have discovered that the recently described Peruvian Pygmy-owl actually appears to constitute two species, one on the Pacific slope and one on the Amazonian, the two differing notably in both morphology and vocalizations.

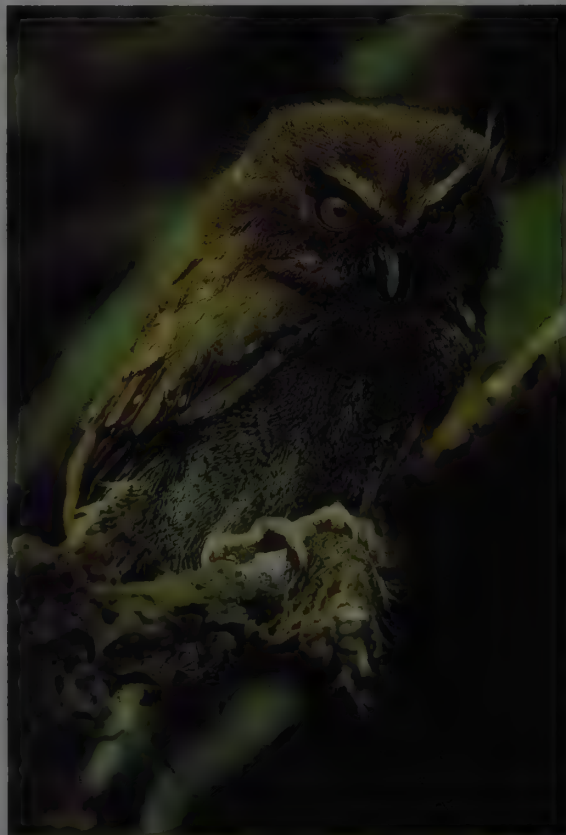
Until very recently, the Least Pygmy-Owl was regarded as comprising eight subspecies, distributed from Mexico to central South America. In contrast to some other *Glaucidium* species, taxa in the *minutissimum* complex do not exhibit plumage dichromatism. S. N. G. Howell and M. B. Robbins revised the taxonomy of this group in 1995, focusing on analyses of vocalizations and plumage. Their work revealed that four species were involved: the Colima Pygmy-owl (*Glaucidium palmarum*) from western Mexico, including the former subspecies *oberholseri* and *griscomi*; the Tamaulipas Pygmy-owl (*Glaucidium sanchezi*) from north-eastern Mexico, previously a subspecies; the Central American Pygmy-owl (*Glaucidium griseiceps*) from south-eastern Mexico to northern South America, including the former subspecies *rurum* and *occultum*; and, finally, the Least Pygmy-owl from south-eastern Brazil and adjacent Paraguay. Howell and Robbins also placed the newly described Amazonian Pygmy-owl from Brazil and the Subtropical Pygmy-owl (*Glaucidium parkeri*) from Ecuador and Peru in the *minutissimum* complex. The first of these was not considered

part of the *minutissimum* complex by König (see above), but Howell and Robbins placed it there on the basis of plumage, size and distribution and in recognition of the variation in vocalizations exhibited by members of the complex. Thus, even with data on vocalizations, the taxonomic status of some *Glaucidium* owls may be far from clear!

Another difficult group is that which includes the Mountain Pygmy-owl (*Glaucidium gnoma*). This species was formerly considered to consist of seven subspecies ranging from south-western Canada to Honduras, but differences in plumage and vocalizations have led several authorities to split it into four species: the Northern (*Glaucidium californicum*), the Mountain, the Guatemalan (*Glaucidium cobanense*) and the Baja Pygmy-owls (*Glaucidium hoskinsii*). The first two range from south-western Canada to the south-western USA and from northern Mexico to Central America, respectively, with the Guatemalan species in the highlands of southern Mexico and Guatemala, and the Baja Pygmy-owl confined to Baja California Sur, in Mexico. The present treatment of the *gnoma* complex is based largely on the recent work of P. Heidrich and associates and of S. N. G. Howell and S. Webb. Genetic analyses support the split of *gnoma* and *californicum*, and work that is currently under way is certain to shed further light on species limits in this difficult group.

The Eurasian Pygmy-owl (*Glaucidium passerinum*) is the only *Glaucidium* in the western Palearctic and has the northernmost distribution of any member of its genus. Because of its similar appearance to the Northern Pygmy-owl of temperate North America, the two have been considered conspecific by some authorities. However, DNA studies have shown that the Eurasian species is much more closely related to the Pearl-spotted Owlet (*Glaucidium perlatum*) of sub-Saharan Africa than to the Nearctic species.

Athene, the last genus in the tribe Surniini, consists of four short-tailed, plump species. The Burrowing Owl is widely distributed in the New World and differs from other *Athene* in having longer legs and a decidedly terrestrial way of life: it inhabits grassland and savanna from southern Canada to the tip of South America and nests below ground in the burrows of fossorial mammals. The Burrowing Owl is often placed in the monotypic ge-



Intensive field research in the last decade of the twentieth century has led to the discovery of a comparatively large number of new taxa of Strigidae. One example is the Peruvian Pygmy-owl. Described as recently as in 1991, it has already been found probably to comprise two distinct species, which differ notably in both voice and morphology. The name "peruanum" is applicable to birds of the amazonian slope, like this one, while the description of the pacific-slope taxon is currently in the process of being done.

[*Glaucidium peruanum*, El Tambo, east of Salinas, Guayas, Ecuador. Photo: Robert Behrstock]

It is not only new species of owl that have been discovered in recent years. Even some genera remained unknown until relatively late, and this was the case with the Long-whiskered Owlet of the Andean slopes of northern Peru. This very rare but highly distinctive, tiny bird, with extremely long facial whiskers, was not discovered until 1977. It is so unlike any other strigid in its morphology that it is afforded its own monotypic genus.

[*Xenoglaux loweryi*, Abra Patricia, San Martín, Peru. Photo: John P. O'Neill]

nus *Speotyto*, but osteological similarities, as well as similarities in outward appearance and in nucleotide sequences, warrant its placement in *Athene*. The Little Owl occurs in desert and semi-open country throughout the Palearctic Region; it forms a superspecies with the Spotted Owlet (*Athene brama*) of India and Indochina. Last but not least, the rare and little-known Forest Owlet (*Athene blewitti*) occurs in deciduous forest in India. Known from only a handful of specimens, and formerly considered extinct, it was rediscovered in 1997 after an "absence" of more than 110 years (see Status and Conservation).

The four species of the saw-whet group, genus *Aegolius*, are small, short-tailed, tuftless owls that inhabit woodland. The sole members of the tribe Aegoliini, they exhibit a striking asymmetry in the size and shape of their ear openings (see Morphological Aspects). The Boreal Owl (*Aegolius funereus*) is Holarctic, whereas the Northern Saw-whet Owl (*Aegolius acadicus*), Unspotted Saw-whet Owl (*Aegolius ridgwayi*) and Buff-fronted Owl (*Aegolius harrisi*) belong to a superspecies complex distributed from central Canada and the USA south through Central America to the southern half of South America. Genetic data indicate that Boreal Owls diverged from Northern Saw-whet Owls about 6 million years ago, and that Buff-fronted Owls shared a common ancestor with the latter. The adult Unspotted Saw-whet Owl bears a striking resemblance to a Northern Saw-whet Owl in juvenile plumage, and it has been suggested that it is a southern race of that species. However, until genetic data are available for the Unspotted Saw-whet, the two taxa are best treated as separate species.

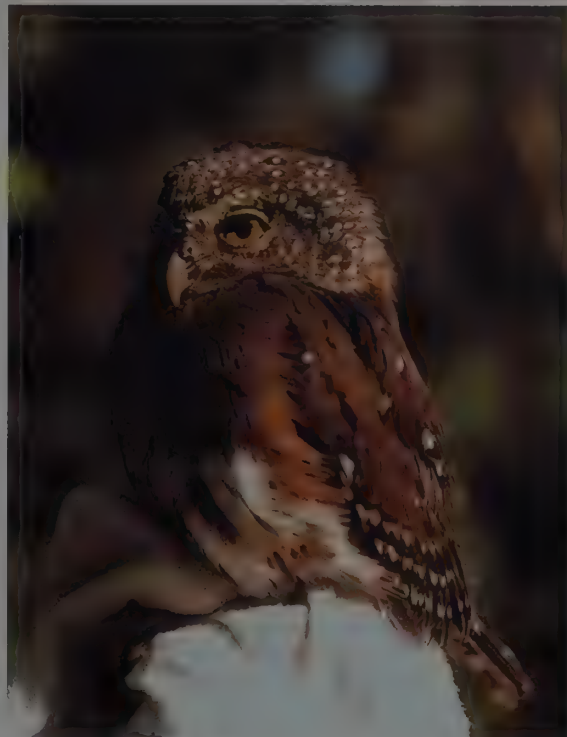
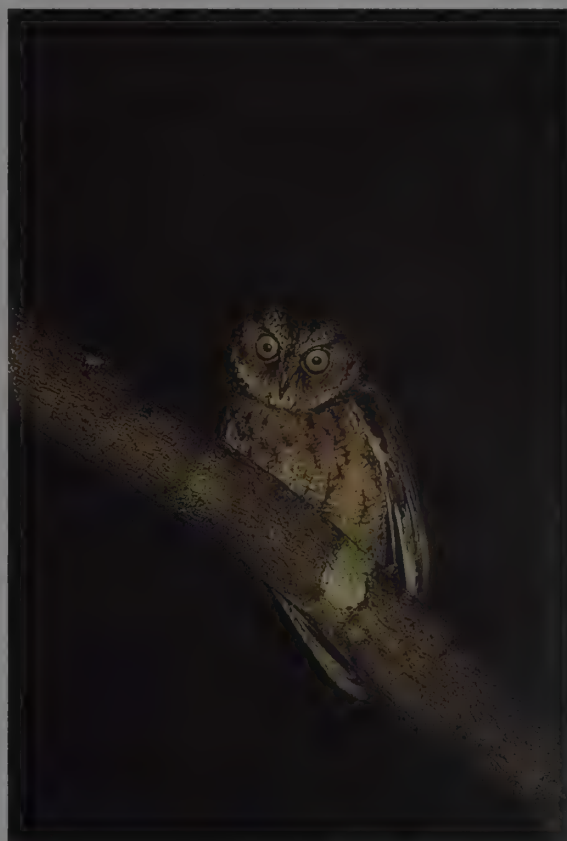
The tribe Ninoxini contains three Old World genera. The 19 species of *Ninox* are confined to the Australasian and Oriental Regions, with two exceptions: the Brown Hawk-owl (*Ninox scutulata*), which extends from India and Indonesia north to Siberia and Japan; and the White-browed Hawk-owl (*Ninox supercilialis*), which is endemic to Madagascar. Aptly known as hawk-owls, the long tail, narrow wings and poorly developed facial disc give some *Ninox* a hawk-like demeanour. The highest diversity of *Ninox* is in Australasia. The three species that are widely sympatric in Australia come in small, medium and large sizes and, accordingly, take different-sized prey. Smallest of them is the Southern Boobook (*Ninox boobook*), with the Barking Owl (*Ninox connivens*) intermediate and the Powerful Owl (*Ninox strenua*) the largest.

Most of the other *Ninox* have restricted ranges that do not overlap with those of their congeners, except for the above-mentioned Brown Hawk-owl. The distribution of taxa in the Bismarck Archipelago and nearby Solomon Islands is especially interesting. The monotypic Manus Hawk-owl (*Ninox meeki*) is the sole *Ninox* on its namesake island group, whereas the larger island of New Britain is inhabited by the monotypic New Britain Hawk-owl (*Ninox odiosa*) and the polytypic Bismarck Hawk-owl (*Ninox variegata*), which also occurs on nearby New Ireland. Just to the south-east, seven subspecies of the Solomon Hawk-owl (*Ninox jacquinoti*) have non-overlapping ranges on the various islands in the Solomon chain. The Christmas Hawk-owl (*Ninox natalis*), endemic to Christmas Island, south of Java in the Indian Ocean, was formerly considered to be a subspecies of the Moluccan Hawk-owl (*Ninox squamipila*), which has its distribution centred some 2500 km away to the north-east of Christmas Island, at the far end of Indonesia. Elevation of the Christmas Island Hawk-owl to a full species was based on recent analyses of mitochondrial DNA and plumage colour and pattern conducted by J. A. Norman and associates. Several other insular taxa in the Moluccan Hawk-owl complex probably warrant species status too (see Status and Conservation), and current research on the Philippine Hawk-owl (*Ninox philippensis*) suggests that at least two species are involved. Overall, *Ninox* remains a very poorly known genus, and future work will no doubt increase the number of species recognized, as evidenced by a new species from Indonesia that has recently been discovered and that is likely to be described before the current year is out.

The remaining members of the Ninoxini are the Papuan Hawk-owl (*Uroglauis dimorpha*) of New Guinea and the Laughing Owl (*Sceloglauis albifacies*) of New Zealand. The strongly barred dorsum and tail of the Papuan Hawk-owl are very similar

to those of the Rufous Owl (*Ninox rufa*), which also occurs in New Guinea; the underparts of the two species differ in being streaked in *Uroglauis* and strongly barred in the Rufous Owl. Sadly, the Laughing Owl may be extinct (see Status and Conservation). It differs from *Uroglauis* and most species of *Ninox* in having long legs and a rather well-developed facial disc.

Asioninae consists of nine species of medium-sized "eared" owls. Despite the paucity of species in the subfamily, the generic limits are unclear. Peters recognized four genera in the group:



Perhaps it is not so surprising that new species of owl are still being named at the very end of the twentieth century. The nocturnal and generally very secretive habits of these birds, in addition to the often remote places in which they live, have effectively protected them from human contact for a prolonged period of time. In 1999, two new species were described for the first time: the Sangihe Scops-owl from the small Indonesian island of that name; and, from the other side of the world, the Cloudforest Pygmy-owl, which is confined to cloudforest on the Pacific slope of the Andes from Colombia to western Ecuador, perhaps extending into northern Peru. Further research will be needed on these newly named species in order to confirm their exact relationships with other members of their respective genera.

[Above: *Otus collari*, Sangihe Island, north-east of Sulawesi. Photo: Frank Lambert.

Below: *Glaucidium nubicola*, Alto de Pisones, Risaralda, Colombia. Photo: F. Gary Stiles]

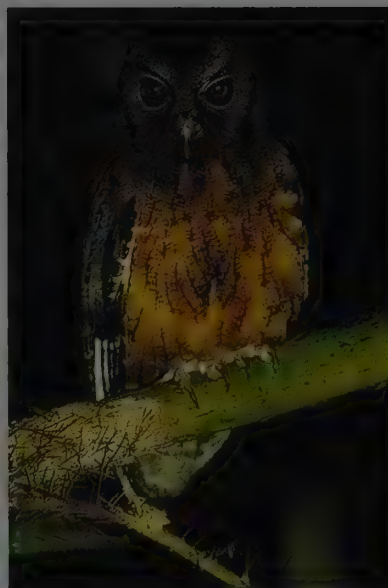
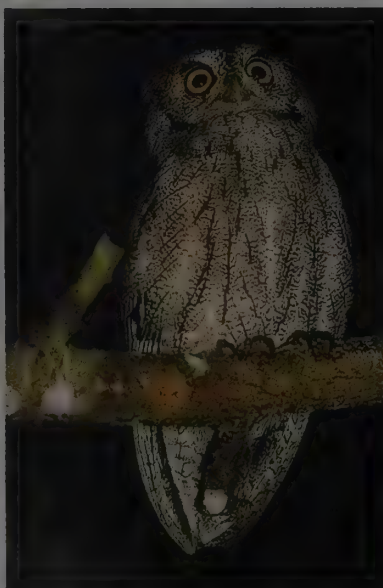


A major taxonomic headache is presented by the genus *Otus*. Not only does it contain a large number of species, some extremely similar to others, but many of its members are very poorly known. In addition, individual variation within species can be rather wide. As a consequence, it is only through intensive research that scientists have been able to determine that some forms should be split as separate species, while others have been "lumped". The six species here are all Neotropical screech-owls.

[Above, left to right:
Otus seductus,
Colima, Mexico.
Photo: R. & N. Bowers/
VIREO.

Otus sanctaecatarinae,
Rio Grande do Sul, Brazil.
Photo: K. Zimmer/VIREO.

Otus vermiculatus
vermiculatus,
Achiote road, Panama.
Photo: Robert Behrstock.



Below, left to right:
Otus barbarus,
Cerro Huitepec
Biological Reserve,
Chiapas, Mexico.
Photo: José Luis Rangel
Salazar.

Otus cooperi cooperi,
Punta Leona,
Puntarenas, Costa Rica.
Photo: Robert Behrstock.

Otus watsonii watsonii,
La Selva Lodge, Ecuador.
Photo: Robert Behrstock]

Rhinoptynx, *Asio*, *Pseudoscops* and *Nesasio*. Ford used cranial characters to merge *Rhinoptynx* and *Pseudoscops* with *Asio*. More recently, Olson identified subtle differences in cranial morphology that separate the more derived *Asio* from the comparatively primitive *Pseudoscops* and *Nesasio*; moreover, he posited that *Rhinoptynx* and *Pseudoscops* belonged together in *Pseudoscops*. Olson's subsequent, albeit unpublished analysis of a specimen of the Stygian Owl (*Asio stygius*) showed it to be allied with *Pseudoscops* as well. In contrast, molecular analyses conducted by Wink and Heidrich indicated that the Striped Owl (*Asio clamator*) and the Stygian Owl belong in *Asio*, which is closer to the more traditional view. Accordingly, the present treatment considers *Pseudoscops* to include only the Jamaican Owl (*Pseudoscops grammicus*), with all other asionine taxa except the Fearful Owl (*Nesasio solomonensis*) placed in *Asio*.

Two of the seven species of *Asio* are widespread in the Old and New Worlds, the Striped and the Stygian Owls are endemic to the Neotropics, and three occur in Africa. The Northern Long-eared Owl occupies grassland, shrubland and open forest throughout the Nearctic and Palearctic Regions, whereas the Short-eared Owl is restricted to open grassland and marshes over much the same range but also occurs in South America. Both species have long wings and light wing-loading, and hunt by coursing low over open country. The African Long-eared Owl (*Asio abyssinicus*) and the Madagascar Long-eared Owl

(*Asio madagascariensis*) constitute a superspecies with the Northern Long-eared Owl; the former is restricted to Central and East Africa and the latter to Madagascar. The Marsh Owl (*Asio capensis*), which occurs in grassland and marshland throughout much of Africa south of the Sahara Desert, is ecologically and morphologically similar to the Short-eared Owl and perhaps is its closest relative.

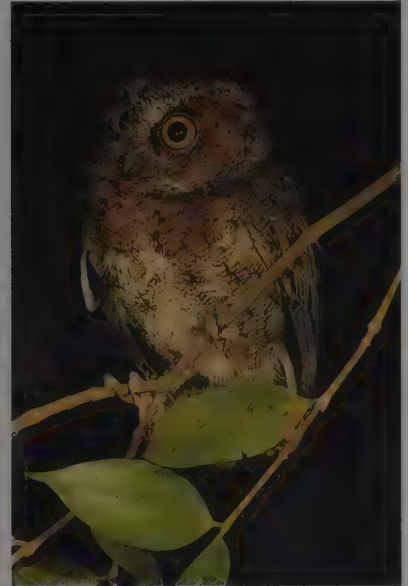
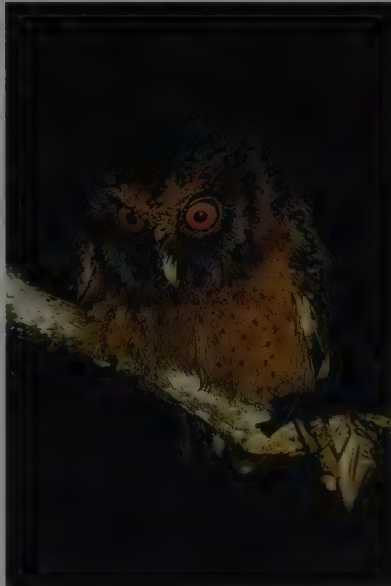
Finally, the Fearful Owl is endemic to the Solomon Islands, and its habits are rather poorly known. It is the only asionine that lacks ear-tufts, and its beak and talons are unusually large for its body size. Presumably, it occupies a niche filled by the larger species of *Ninox* elsewhere in Australasia. Although it is positioned last in the species list of Strigidae, the Fearful Owl perhaps belongs after *Pseudoscops* in recognition of the relatively primitive cranial morphology that it shares with this genus, as opposed to *Asio*.

Morphological Aspects

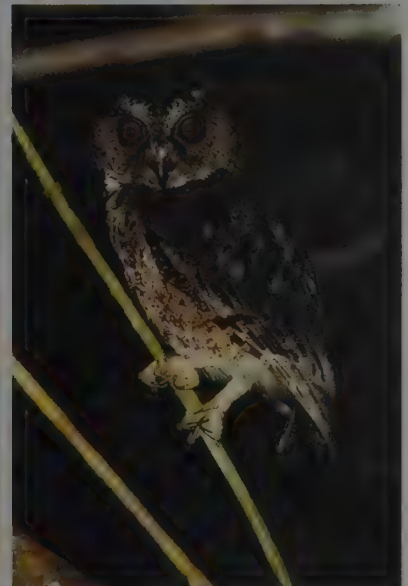
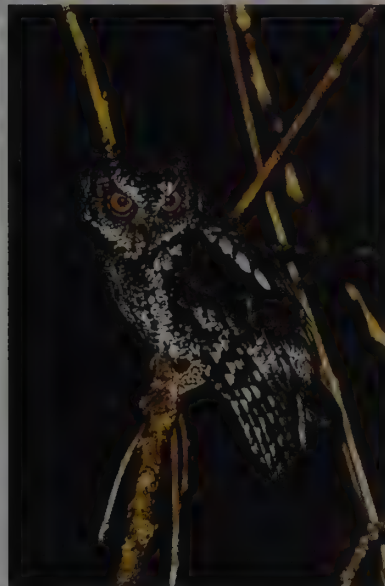
Strigids vary one-hundredfold in body mass, from the tiny Elf Owl to the massive female Eurasian Eagle-owl. Despite this tremendous variation, however, body proportions and basic morphology are rather similar throughout the family. Several distinctive features are found in almost all species. These include

The difficulties in classifying *Otus* species are, if anything, even greater in the Oriental Region. Here, there are many distinct populations of scops-owls which are poorly known, with restricted ranges, but at the same time a fair number of others which are more widespread and highly variable. As with the Neotropical screech-owls, only much further research, especially of vocalizations, will lead to a proper understanding of the taxonomy of this fascinating genus.

[Above, left to right:
Otus rufescens rufescens,
Borneo.
Photo: Michael &
Patricia Fogden.



Otus magicus leucospilus,
near Batu Putih,
Halmahera, Moluccas.
Photo: Frank Lambert.



Otus longicornis,
San Salvador Islands,
Luzon, Philippines.
Photo: Doug Wechsler/
VIREO.

Below, left to right:
Otus mirus,
Mount Apo National Park,
Mindanao, Philippines.
Photo: Doug Wechsler/
VIREO.



Otus manadensis
manadensis,
Dumoga-Bone
National Park, Sulawesi.
Photo: Frank Lambert.

Otus megalotis boholensis,
Bohol, Philippines.
Photo: Pete Morris.]

a large head with a round facial disc encircling the eyes, a moderately short tail, and soft, cryptically coloured plumage. Members of Strigidae differ from those of the other owl family, Tytonidae, in having a round rather than a heart-shaped facial disc, and four rather than two notches in the sternum. Strigids also have a rounder skull with relatively larger orbits, a furcula that is not fused to the sternum, and a naked uropygial gland. In addition, the third toe is longer than the second in strigids, whereas the two toes are equal in length in tytonids, and the nail on the third toe has a smooth cutting edge, as opposed to a comb-like, or pectinate, edge in tytonids.

As would be surmised for an exclusively raptorial family, no extant species is flightless, and flight is the main form of locomotion used during foraging. Some species, such as the Burrowing Owl, are somewhat terrestrial in habits, with longer legs for pursuing insect prey on foot. Others, notably the hawk-owls and pygmy-owls, capture flying birds or, as is often the case in some *Ninox* species, fruit-bats and gliding marsupials, and these owls have relatively long tails for increased agility.

Many owl species with distributions covering a broad range of latitudes conform to Bergmann's Rule, which states that selection favours a larger body at higher, cooler latitudes. The largest Brown Hawk-owls, for instance, occur at the northern end of the species' range in Ussuriland, in the Russian Far East, whereas the smallest are found in the tropical forest of Java.

Similarly, the largest Burrowing Owls occur in southern South America and the smallest on the equatorial savannas of Brazil. In addition, Kelso's Rule was formulated for owls, stating that the feathering on the toes and tarsi is more extensive in species that inhabit high latitudes than in those that occur in lower, warmer latitudes. Indeed, the tarsi and toes of the Snowy Owl have extremely dense feathering, and those of the other Holarctic species also are heavily feathered. In contrast, the feet of many tropical species are sparsely feathered, and those of some, including the Bare-shanked Screech-owl (*Otus clarkii*) and the Colombian Screech-owl, are virtually naked. Kelso's Rule works within species, as well: Barred Owls of the northern, nominate race have dense feathering on their tarsi and toes, whereas the Florida race *georgica* has feathered tarsi but unfeathered toes. Similarly, Stygian Owls from Mexico and Central America, race *robustus*, have sparsely feathered toes, but those from Brazil, the nominate subspecies, have bare toes.

Most of the morphological features distinctive of strigids arise from the fact that they are predatory and nocturnal. These two forces have produced specialized plumage, ears, eyes, bill and feet. Plumage colours are dominated by browns and greys that make most species highly cryptic, presumably to allow the birds to roost undisturbed during the daytime (see General Habits). The plumage colour generally follows Gloger's Rule, with dark brown colours in humid climates, as shown for example by



Crested and Spectacled Owls in Neotropical rainforest, and sandier tones in arid areas, as illustrated by Hume's Owl of the deserts of Arabia and other parts of the Middle East. Again, the trend also holds within species. This is demonstrated, for instance, in the Northern Saw-whet Owl, where the dark brown race *brooksi* occupies the temperate rainforest of the Queen Charlotte Islands; it is also reflected by the pale forms of the Little Owl and Eurasian Eagle-owl in the more arid portions of Eurasia.

Because most owl species are active only at night, sexual-selection pressure for the colourful plumages typical of many males of other bird groups is largely absent. The Snowy Owl, which breeds during the 24-hour daylight of the Arctic summer, shows the most sexual dimorphism in colour, with adult males essentially pure white and adult females and immatures speckled and barred with dark brown. Subtle differences between the sexes in plumage colour occur in a few other species, such as the Northern Long-eared, Marsh and Short-eared Owls, in which females are darker and rustier than males, particularly on the tarsus, belly, underwing and facial disc, and in the Burrowing Owl, females of which tend to be darker and more heavily marked than males.

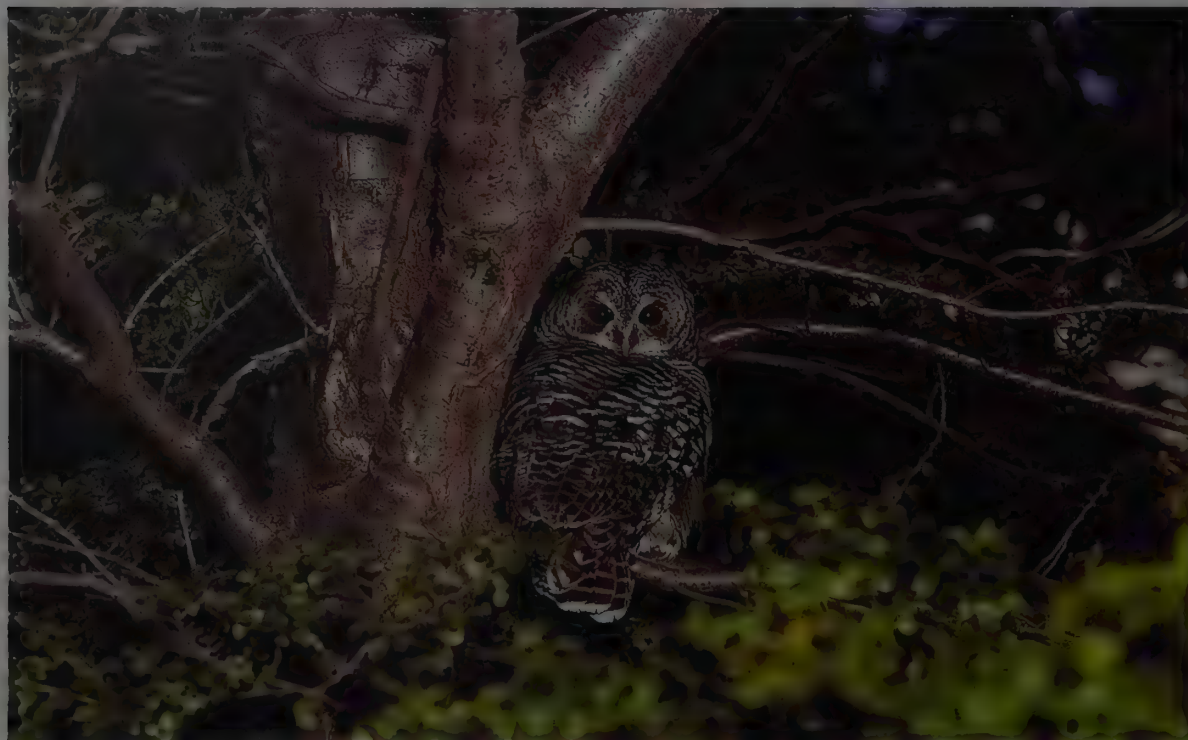
Owl feathers lack an aftershaft but have a downy base. The flight-feathers are covered with a velvety pile that is very soft to the touch, quite unlike the stiff, glossy feel of the flight-feathers of most other bird species, and in many strigids the leading edges of the outer primaries have a short, comb-like fringe that deflects air upwards as it passes over the wings during flight. These two features apparently combine to produce the silent flight so typical of owls, allowing them to fly towards prey using auditory cues that would normally be obscured by the sound of flapping wings. Largely diurnal species such as some *Glaucidium* lack the comb-like fringe on their primaries, as do *Ketupa* and *Scotopelia* owls, and the flight of these species is not as quiet as that of other owls. W. Neuhaus and colleagues, however, report that experimental removal of the comb-like fringe on the primaries of species normally possessing it had no effect on wing noise during flight.

The silent flight of owls is probably enhanced by the light wing-loading typical of the family. Most owls have large wings in relation to their body mass. In some species, such as most *Asio*, this is clearly an adaptation for spending long periods of time flying in search of prey, whereas in others it may simply make it easier to fly silently and with agility. Species that hunt from a perch generally have rounded wings, and those that course over fields have longer, less rounded wings.

Owls in temperate regions replace their feathers in summer and autumn, whereas tropical species have more extended or year-round moulting regimes. The Eurasian Scops-owl suspends moult of its flight-feathers during migration and completes it on the wintering grounds, but the closely related Flammulated Owl of North America seems to complete its flight-feather moult on the breeding grounds. Many owls shed all of their rectrices nearly

The White-throated Screech-owl appears to be an aberrant form of Otus, lacking the ear-tufts so typical of that genus. Indeed, some taxonomists believe that it should not be included in Otus at all. Although DNA studies have shown this species to be quite closely related to the other New World screech-owls, it may perhaps be better placed in a separate genus, or subgenus, Macabra.

[*Otus albogularis*, Peru.
Photo: John O'Neill]



Despite an enormous variation in size and weight, the strigids share a similar basic morphology, typified by the Rufous-legged Owl. With few exceptions, they all have a large, fairly rounded head, a relatively short tail and, perhaps most distinctive of all, a rounded facial disc with large eyes. In most cases, the plumage is soft and markedly cryptic, effectively concealing the birds at their daytime roosts.

[*Strix rufipes rufipes*, Patagonia, southern Argentina.
Photo: François Gohier]

Large, broad, rounded wings characterize the majority of the Strigidae. The flight-feathers are covered with a very soft, velvety pile which, together with a peculiar comb-like structure along the leading edge of the outer wing of most species, produces a totally silent flight, although the exact role played in this by the comb-like primary fringe is uncertain. A further characteristic of the family, visible on this Spotted Eagle-owl, is the sharp, curved talons, a vital adaptation since all strigids catch their prey with the feet.

[*Bubo africanus africanus*,
Helderberg Nature
Reserve, South Africa.
Photo: Peter Steyn/Ardea]



simultaneously or over a period of a few days, leaving them tail-less for a short time after the breeding season.

In some genera, for example *Athene*, the post-breeding or pre-basic moult is complete, but many species have an incomplete moult of the primary and secondary feathers. Some captive Boreal Owls, for example, have been known to retain a few juvenile primaries for up to five years. As a result, complex patterns of different-aged remiges are often present on the wings of adults. The extent of remigial moult is related to breeding effort in the Ural Owl (*Strix uralensis*); H. Pietiäinen and associates found that the number of flight-feathers an individual replaced each year was inversely related to the number of young it had raised that season, and non-breeders moulted the largest number of flight-feathers.

Age-related differences in plumage, if present at all, are usually subtle. The genera *Ptilopsis*, *Glaucidium* and *Aegolius*, however, have non-downy juvenile plumages that are distinctly different from those of the adults. Indeed, the juvenile Northern Saw-whet Owl was initially described as a different species, the "White-fronted Owl". The plumages of immature Snowy Owls are generally more heavily barred with brown than their adult equivalents. Several species show changes in the pattern of tail barring between yearling and adult birds, the adults generally having fewer and wider bars; the Great Horned, Spotted, Barred and Northern Long-eared Owls come in this category.

Dark nape patches, in the form of two spots of dark feathers edged in white, which thus resemble eyes, are a remarkable plumage pattern found in many *Glaucidium* owls and in the Northern Hawk-owl. These species are active during the day, and the "false eyes" presumably fool larger predators such as hawks (Accipitridae), and perhaps smaller mobbing birds, into thinking that the owls are always watching them and are therefore aware of their presence. The fact that some *Glaucidium* species have this plumage pattern and others do not is interesting. Whether its presence relates to size (several of the species lacking the pattern are relatively large), behaviour, or simply a shared evolutionary history is unknown. Two of the species that do not possess "false eyes", the African Barred Owlet (*Glaucidium capense*) and the Sjöstedt's Owlet (*Glaucidium sjostedti*), are partly nocturnal. Others lacking the pattern, such as the Asian Barred Owlet (*Glaucidium cuculoides*), are largely diurnal, but they may share

the African Barred Owlet's habit of hunting from more hidden perches in denser forest and would thus be less prone to discovery by would-be predators or mobbing passerines. All of the New World *Glaucidium* have the "false eyes".

Some nocturnal birds, notably a few of the tropical caprimulgids (see page 309), have evolved spectacularly long streamers on their wings or greatly elongated tail feathers for use in courtship and territorial displays, but such dramatic structures are lacking in strigids. Many strigids do, however, have a plumage feature that alters their silhouette: the so-called "ear-tufts" on the head. Well-developed ear-tufts are restricted to nocturnal species, lending some credence to the theory that they function primarily to camouflage owls on daytime roosts: raised ear-tufts break up the outline of a roosting owl and enhance the impression that the cryptically coloured bird is part of the tree in which it is perched. Some researchers have suggested that these tufts are used for behavioural signalling and species recognition, but these proposals remain speculative. Ear-tufts are common among the Striginae and the Asioninae, but more or less lacking in the Surniinae. Nevertheless, many species without noticeable ear-tufts, such as the Snowy Owl and some *Glaucidium* and *Aegolius* owls, raise the feathers at the corners of their forehead when excited (see General Habits), and this can give the impression of small ear-tufts.

Perhaps the most distinctive feather structure associated with owls is the facial disc. This is composed of feathers with very open vanes and it lies over paired (one on each side of the face) layers of densely packed feathers with large rachides and reduced vanes. The latter layers are termed the facial ruff and are clearly associated with hearing. They are inserted behind the ear openings in a special flap of skin, and they form more or less solid, roughly parabolic troughs surrounding and leading to the ear openings themselves. The facial ruff, and the facial disc that covers it, are very large in highly nocturnal species such as the Buff-fronted Owl, and in species that can detect prey under the snow, such as the Great Grey Owl; they are smaller and less well developed in diurnal or crepuscular species such as the Snowy Owl, *Ninox*, the Northern Hawk-owl, and *Glaucidium* species, all of which hunt more visually. The facial ruff may provide a tenfold increase in the sound pressure delivered to the ears, and it probably has an important function in sound localization as well. The motor muscles associated with the skin around the ear

openings probably allow owls to change the shape of the facial ruff, directing it towards sounds in the same manner as many mammals move their external ears.

The hearing of owls is more sensitive to low-frequency sounds than is that of most birds and is sensitive across a wide range of frequencies. Most strigids have excellent sensitivity down to at least 250 Hz, and their high-frequency threshold ranges from about 7 kHz in the Great Horned Owl to 11 kHz in the Northern Long-eared Owl and the Mottled Owl. The frequency at which owl hearing is most sensitive ranges from 500 Hz in the Great Horned and Mottled Owls to 6 kHz in the Northern Long-eared Owl, the African Wood-owl and the Tawny Owl.

In most owls, the external ear openings are very large and are surrounded by folds of skin with associated motor muscles. These openings are long, crescent-shaped structures that are quite different from the tiny circular openings found in other birds. At least five genera, comprising four separate phylogenetic lines, have asymmetrical external ears in which the right and left ear openings are different in size or shape or both. This phenomenon is seen in *Bubo*, *Strix*, *Aegolius*, *Pseudoscops* and *Asio*. The asymmetry is restricted to the fleshy parts of the ear openings in *Bubo*, *Pseudoscops*, *Asio* and most *Strix*, but in *Aegolius* and in two species of *Strix*, the Ural and Great Grey Owls, the bony structure of the ear is markedly asymmetrical as well.

In *Aegolius*, the slit-like ear openings in the skin are symmetrical and extend the full height of the skull. The actual openings into the skull, however, are only half the size of the slits in the skin and are highly asymmetrical. The opening on the right is about 6 mm higher than that on the left. In the Boreal Owl, the right ear is up to 50% larger than the left and is directed upwards, whereas the left ear is directed downwards. The skull asymmetry in *Strix* and *Aegolius* does not extend to the middle and inner ears. In Marsh Owls and other members of the genus *Asio*, the right and left ear openings are of the same size and shape but are situated in different vertical positions on the head. The remarkable asymmetry in ear size and shape enables these owls to localize sounds in the vertical as well as the horizontal plane, thus allowing them to determine the exact location of prey by sound alone. For example, Great Grey Owls can pinpoint and

capture mice under 45 cm of snow, and fossorial rodents beneath more than 2 cm of soil.

Owls use differences in interaural time and interaural intensity to localize the horizontal direction (azimuth) of a sound. In other words, they compare the time at which a sound arrives in the left ear with the time when it arrives in the right ear, as well as how loud the sound is in each ear. To localize sounds in the vertical plane, owls compare the intensities of high-pitched sounds in each ear. These sounds must have wavelengths about equal to or shorter than the size of the ear openings; for most owl species, this corresponds to sounds above 5 kHz. Localization is also more accurate if the sounds are complex, consisting of a number of tones with very different wavelengths. Consequently, the rustling sounds made by small mammals in forest leaf litter are ideal for localization by owls.

The Strigidae have relatively large eyes. Indeed, those of some species are larger than the human eye, and even the eye of the medium-sized Tawny Owl is longer than that of a human being. Owl eyes are distinctly tubular in shape and have a lens that is more spherical than that of other birds, so as to maximize retinal image size. The eyes are positioned well apart and on the front of the face, which is flattened in owls, resulting in excellent depth perception. The eyes of a Tawny Owl diverge at an angle of 55°, giving a binocular field of view of 48° and an overall visual coverage of 200°. Owls have not maximized their binocular field of view; to do so would reduce the total visual field to 120°. The accuracy of depth perception through binocular vision is often augmented by owls through head-bobbing and head-weaving. The neural pathways involved in binocular vision have been studied for the Little Owl by P. Bagnoli and V. Porciatti and their respective co-workers, and for the Northern Saw-whet Owl by D. Wylie and associates. These systems are more highly developed in owls than in other birds such as pigeons (Columbidae) and chickens, and they exhibit strong convergence with the condition found in frontally eyed mammals such as monkeys and humans.

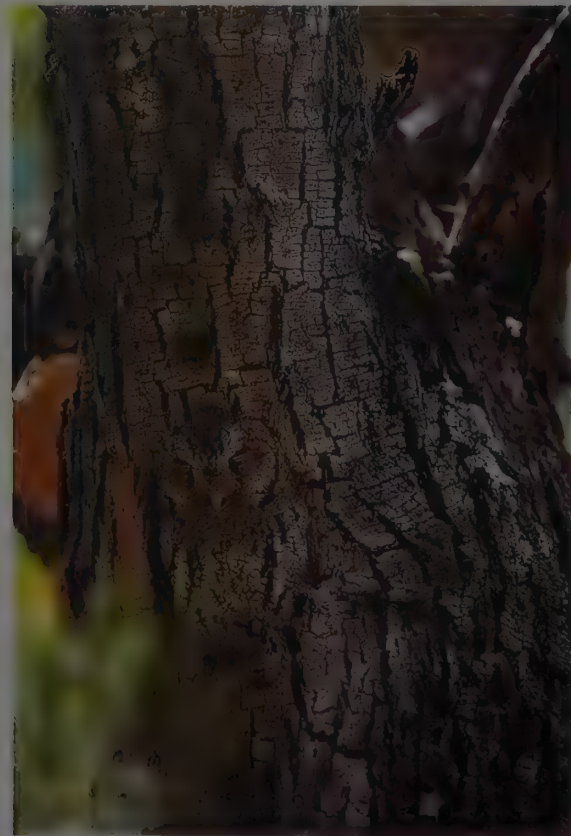
All birds' eyes are more or less fixed in their orbits, fully enclosed by the bones of the skull, and their movement is restricted to less than 1° of arc. The relatively long, tubular eyes of owls project well beyond the skull, but are supported by a ring of bony plates called the sclerotic ring. The immobility of the eyes, combined with their forward-pointing aspect, means that an owl has to turn its head to see objects to the side or behind it. To do this, the perched owl can rotate its head more than 270°, a trait that many people consider remarkable. However, a highly flexible neck is not at all unusual among birds, because it is an essential part of their ability to fly. Indeed, recent studies by K. P. Dial and colleagues have shown that, during flight, birds commonly rotate the body through 270° or more while keeping the head level.

Contrary to popular belief, owls cannot see well in extremely dark situations, and they have no difficulty whatsoever in seeing during daylight hours. G. Martin has established that the mean absolute visual threshold, that is the minimum amount of light required to see objects, is about two times lower in Tawny Owls than in humans. The level of variation, however, is such that the most sensitive human eyes would be equal to or better than the least sensitive owl eyes in this regard. Owls fare rather better when compared with diurnal birds such as pigeons, where a hundredfold difference exists in visual sensitivity in low light. Unlike many nocturnal mammals, owls lack a tapetum in the retina, as do all other birds except the caprimulgiforms. The tapetum is a structure that can improve visual sensitivity at night by a factor of about two. Thus, a typical nocturnal mammal such as a house cat has a mean absolute visual threshold about 2.2 times lower than that of a Tawny Owl.

The daylight visual acuity of owls, about 2.5 to 5 minutes of arc, is similar to that of most other birds and better than that of many nocturnal vertebrates such as cats and rats, but it is about five times lower than that of humans and diurnal raptors. Much of the improved visual performance of owls in low light conditions is due to their large pupils. The focal lengths of the eyes of humans and Tawny Owls are very similar, but the larger pupil diameter of the owl creates an image that is about 2.7 times

The amazingly cryptic plumage of strigid owls could not be better illustrated than it is in this shot. A Flammulated Owl sleeping by day in a tree cavity merges so perfectly with the background of the tree's bark that it would pass unseen by all but the most discerning of human eyes. This remarkable camouflage, arising from both the coloration and the pattern of the plumage, also serves to conceal these nocturnal birds from diurnal predators, as well as from the mobbing attentions of smaller birds.

[*Otus flammeolus*, Madera Canyon, Arizona, USA. Photo: Sid & Shirley Rucker/DRK]



The extreme in pale coloration among owls is found, predictably enough, in the Snowy Owl of the circumpolar Arctic. Adult males are essentially pure white, while adult females and immatures, although barred and spotted with dark brown, still appear exceedingly pale.

Note also the densely feathered tarsi and feet of this individual as it balances, wings spread, on a stump amid green grass: in accordance with Kelso's Rule, the toe and tarsal feathering is more extensive in species of colder, higher latitudes than in those inhabiting warmer, lower ones.

[*Nyctea scandiaca*,
British Columbia, Canada.
Photo: Tim Fitzharris/
Minden Pictures]



brighter than the one perceived by the human eye. For those familiar with a camera lens, the Tawny Owl eye has an f -number of about 1.3, compared with an f -number of 2.1 for a human. This improvement in light-gathering in the owl eye is sufficient for the owl to avoid branches and other obstacles in low light conditions, but it is not enough to allow the owl to see all objects below the forest canopy on a moonless night. Consequently, forest owls must rely on spatial memory to avoid obstructions, or else they probably restrict their activities to the crepuscular hours or to moonlit nights when the light is better.

Owls have a duplex retina that contains both rod and cone receptors. In the retinas of most birds, cone cells far outnumber rod cells, but the owl retina contains many more rods than cones. In the Barred Owl, for example, the ratio of rods to cones is about 10:1. Rod cells are more sensitive to low light, but they give very poor, if any, colour vision. In the vertebrate retina, fine spatial resolution is generally mediated by the fovea. Owls have an unusual mixed fovea that contains both cone cells and rod cells, instead of being composed of cone cells alone. Therefore, they have some ability to see colours, but surely not to the extent of most diurnal birds. For instance, experiments conducted by G. Martin have shown that the Tawny Owl "has a fully functional colour vision system, but one perhaps less capable of making colour discriminations as fine as can be achieved by the pigeon". Little Owls apparently confuse red with dark grey, and electro-retinogram studies by V. Porciatti and colleagues have confirmed the dominance of rod cells in this species. Given their limitations in colour perception, one must wonder why so many strigids have brightly coloured irides.

An owl's bill is rather short and stout, with a sharply hooked upper mandible and sharp cutting edges. The depressed shape may be an adaptation to maximize the field of view for the forward-pointing eyes. The cere is overlain by thick bristles that also point forwards. Owls have zygodactyl feet, the fourth toe being reversible so that the second and third toes face forwards and the first and fourth face backwards. This character is perhaps advantageous when holding prey, although it is not found in the other major group of raptorial birds, the hawks, eagles and falcons (Falconiformes). It is more likely that zygodactyl feet are an adaptation for perching on branches. In *Ketupa* and *Scotopelia* owls, the scales on the soles of the feet are modified into spicules

to aid in holding their slippery piscine prey. Many insectivorous species have unfeathered, rather delicate toes, as opposed to the heavily feathered, powerful toes with heavy talons present on carnivorous species. Pygmy-owls have relatively long toes tipped with long talons that allow them to capture prey up to their own size and larger (see Food and Feeding).

In contrast to the Snowy Owl (*Nyctea scandiaca*), the Jungle Hawk-owl is one of the darkest of all strigids, as befits its humid rainforest habitat. This is a demonstration of Gloger's Rule, with darker plumages found in humid climates and paler ones in drier habitats. The genus *Ninox*, which makes more use of visual cues in hunting, has a less well-developed facial disc than most owls, as also do diurnal species such as the Snowy Owl and *Glaucidium* species.

[*Ninox theomacha*
theomacha,
Tari valley,
Papua New Guinea.
Photo: Don Hadden/
Ardea]





A particular feature of the Strigidae is the occurrence in many species of polymorphism, a phenomenon especially marked among the *Otus* owls. The Guatemalan Screech-owl, here in its grey-brown morph, occurs also in a rufous morph, and the Vermiculated Screech-owl, shown in its rufous morph, also has a grey-brown morph. Formerly thought conspecific, these two species have been shown to differ vocally and in the extent of their tarsal feathering.

[Left: *Otus guatemalae guatemalae*, Tikal National Park, Guatemala. Photo: Robert Behrstock.

Right: *Otus vermiculatus vermiculatus*, La Selva Biological Station, Costa Rica. Photo: José Luis Rangel Salazar]

Food ingested by owls passes through the oesophagus into the glandular stomach (proventriculus), then into the muscular stomach or gizzard. Unlike many other bird groups, owls lack a true crop or other dilation of the oesophagus. Food is retained in the stomach for three to 13 hours. Then, 10-12 minutes of vigorous gastric contractions force the liquid digesta into the duodenum while compacting the undigested material that remains in the gizzard. The solid material, consisting of bones and hair if the food was mammalian, bones and feathers if avian, and chitin if from invertebrates, is squeezed into an ovoid pellet and forced back up into the lower oesophagus. From there, the pellet moves upwards by reverse peristalsis and is ejected from the wide-open mouth, this event often being accompanied by convulsions and vigorous shaking of the owl's head.

Owls generally produce one pellet per meal, but some pellets may contain the remains of several prey items that were eaten in quick succession. D. Chitty, working with captive Short-eared Owls, has shown that the time interval between a meal and pellet production is correlated with meal size; a pellet was produced within three hours after a meal of 10 g, but it took eight hours to produce a pellet after a meal of 40 g. G. E. Duke and associates found that the meal-to-pellet time interval was shortened in captive Great Horned Owls that were fed in the morning rather than in the evening, and also when the owls could see other conspecifics. It was not shortened, however, if the owls were presented with food before they had finished digesting an earlier meal.

Owl pellets contain about ten times as much bony material as those ejected by diurnal birds of prey such as hawks. They therefore provide an ideal means of studying food habits (see Food and Feeding). The relatively high amount of bone in their pellets results in part because owls are less able than hawks to digest bone. The gastric fluid of owls has a pH of about 2.35, compared with 1.6 in hawks. Because pH measures the logarithm of the reciprocal of hydrogen ion concentration, the gastric juice of hawks is about six times more concentrated than that of owls. In addition, owls appear to be more likely than hawks to swallow their prey whole, which means that they ingest more bones with their meal.

Interestingly, owls that hunt on the wing may have a smaller digestive tract than those that hunt from perches. N. W. Barton and D. C. Houston found that the Northern Long-eared Owl, whose foraging habits are typically more aerial, has a significantly lighter digestive tract and a shorter small intestine than does the perch-hunting Tawny Owl. Presumably, this reduction in mass is an adaptation to reduce flight costs in Northern Long-eared Owls.

A particularly interesting aspect common to most owls and diurnal raptors is that they exhibit reversed sexual dimorphism in size, often referred to as "RSD", whereby females are generally larger than males in structural characters and body mass. The difference is greatest in species such as the Mottled, Great Grey and Boreal Owls, in which the females can weigh about 40% more than the males. There are a few exceptions to this pattern of reversed size dimorphism. In at least one New World species, the Burrowing Owl, the male is slightly larger than the female, and males also are larger than females in the Rufous, Powerful and Barking Owls and the Papuan Hawk-owl.

More than 20 theories have been advanced to explain reversed sexual size dimorphism in birds. Several of them flow from the strict division of labour in owl breeding biology. For instance, because only females incubate the eggs and brood the young, selection could act to produce larger females that could brood more efficiently. In general, RSD seems to be higher in species that eat vertebrate prey, such as *Bubo*, *Strix* and *Aegolius*, and lower in insectivorous species such as the screech-owls and scops-owls of the genus *Otus*. E. Korpimäki has suggested that it is advantageous for female Boreal Owls to be large so that they can survive periods of food shortage, whereas the males, being small and agile, can hunt more efficiently and effectively. Although the argument for small males may hold, H. C. Mueller has stated that females of all sizes can simply increase their fat reserves to survive periods of food shortage. Moreover, R. P. and D. M. Gerhardt point out that the owl species with the highest known sexual dimorphism in size, the Mottled Owl, is not only insectivorous but also lives in tropical forest, where food shortages are probably rare or non-existent.

W. B. McGillivray's analysis of reversed sexual size dimorphism in owls led him to conclude that the phenomenon was unlikely to result from ecological forces such as differential foraging between the sexes. He pointed out, for instance, that the Snowy Owl and the Short-eared Owl have relatively similar foraging and migration strategies but strikingly different dimorphism indices. McGillivray also found no strong evidence of shape differences between males and females that would have resulted from selection for different foraging strategies. The maze of theories surrounding RSD is further complicated by the conflicting data that emerge when one considers different body-size variables such as mass, wing length, and the dimensions of various bones. Several investigators contend that wing length and body mass are poor variables to use, because the former can be difficult to measure and varies owing to feather wear, whereas the latter is highly variable among seasons. Moreover, mass data are often taken from museum specimens dominated by birds that have been found emaciated in winter, or are gathered from breeding studies, when female owls can be 50% heavier than at other times of the year.

After examining all of the current theories, Mueller felt that many factors could affect the amplitude of dimorphism, but that the only one that could explain the origin of the phenomenon was female dominance and the establishment of the pair-bond. This theory holds that dimorphism results from sexual selection in which females choose males that are smaller and, presumably, less aggressive. This is, of course, the opposite of what happens in the other form of sexual size dimorphism in birds such as grouse (Tetraonidae) and pheasants (Phasianidae), in which females apparently choose the larger, more dominant males.

Habitat

Strigids occupy virtually all of the world's major terrestrial habitats, being absent only from extremely high elevations and treeless portions of harsh deserts such as the Sahara. They occur on every continent except Antarctica, and one species, the Short-eared Owl, has colonized some of the most remote oceanic islands in the world. Still another, the Burrowing Owl, spends part of its life underground. By far the majority of species, how-

ever, roughly 95%, reside in forest of one kind or another. As is true for almost any species of bird, the chief factors that dictate habitat use by owls are food and nest-sites. The latter are especially critical for strigids, because they do not build their own nests, relying instead on natural sites or existing structures built by other bird species (see Breeding). Although basic information on habitat associations is known for many owls, studies of actual habitat use have been conducted on only a handful of species. Consequently, few details are available on how owls exploit the habitats they occupy, how and where they obtain food, and how habitat use varies seasonally.

Not surprisingly, the highest number of owl species occurs in tropical forest. Indeed, approximately 80% of the world's strigids can be found in the tropics: 28% in Central and South America, especially *Otus*, *Glaucidium* and *Strix*; 25% in Asia, represented by *Otus*, *Glaucidium*, *Bubo* and *Ketupa*; 19% in Africa, notably *Ptilopsis*, *Bubo* and *Scotopelia*; and 8% in Australasia, all *Ninox*. Within this belt of latitude, however, owls occupy a wide variety of wooded habitats that range from dense lowland jungle to second-growth forest, savanna, plantations and arid scrubland.

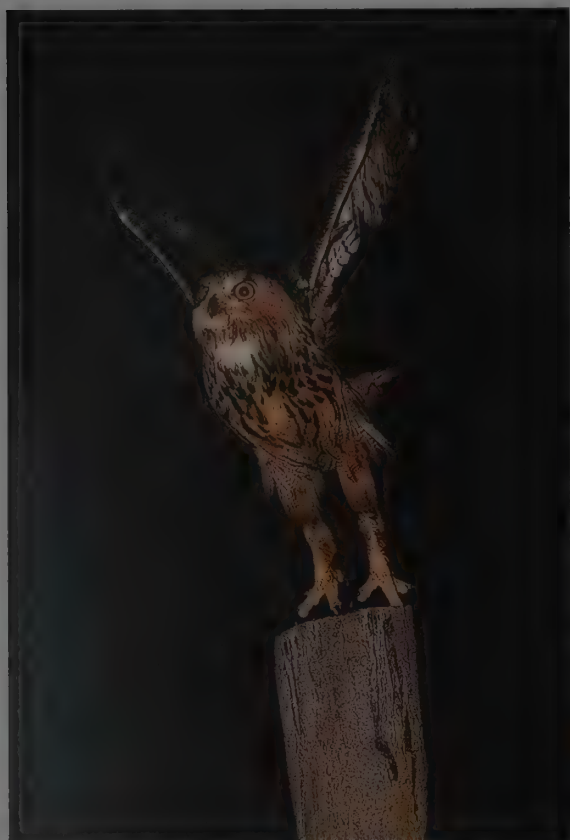
High-elevation cloudforest in the New World tropics supports a luxuriant growth of vegetation and a high diversity of owls. The steep, mountainous terrain characterized by this habitat can be of difficult access for humans, and can also be prone to natural habitat fragmentation. Thus, some of the species that are tied to cloudforest are known only from very small ranges. For example, the Bearded Screech-owl (*Otus barbarus*) inhabits a restricted zone of cloudforest in southern Mexico and northern Guatemala. Two recently described species, the Cinnamon Screech-owl and Hoy's Screech-owl, (*Otus hoyi*), are restricted to the Andes of, respectively, southern Ecuador to northern Peru and southern Bolivia to north-western Argentina. The newly described Cloudforest Pygmy-owl (*Glaucidium nubicola*) is known only from the west slope of the Andes in Colombia and Ecuador. Perhaps the most mysterious strigid of the South American cloudforest is the rare and distinctive Long-whiskered Owlet, which has so far been encountered only in a remote region of northern Peru.

Four screech-owls that inhabit South American cloudforest more or less replace each other along an elevational gradient. The most widespread of these, the Tawny-bellied Screech-owl,

Age-related plumage differences tend to be rather minor among most owls, and juveniles, once they have lost the last vestiges of down, are often extremely difficult to separate from adults of their species. There are, however, some exceptions, one of the most striking of which is shown by the aptly named Spectacled Owl. The juvenile lacks the adult's dark brown head and breast with distinctive pale "spectacles", instead having a pale, almost whitish head and body with a conspicuous dark heart-shaped "eye-mask". This species can take up to five years to reach full adult plumage.

[*Pulsatrix perspicillata*,
Costa Rica.
Photo: Michael &
Patricia Fogden]





occupies lowland rainforest across Amazonia but extends its range upwards on the eastern face of the northern Andes. In the Andes it is replaced in elevation by the Rufescent Screech-owl, which occupies a narrow band of cloudforest from Venezuela to Bolivia. Occurring higher still is the Cloudforest Screech-owl, known only from dense mountain forest in south-central Peru. Finally,

the White-throated Screech-owl (*Otus albogularis*) has a distribution very similar to that of the Rufescent Screech-owl, except that it occurs at higher elevations and occupies stunted alpine forest and forest edges, as well as cloudforest. Other cloudforest species that occur in much of the northern Andes are the Rufous-banded Owl and the Andean Pygmy-owl.

Dense lowland rainforest in the New World tropics supports a diverse suite of species that includes the Crested, Spectacled, Tawny-browed and Black-banded Owls. Also occurring in this habitat, but occupying a variety of forest types in addition to primary rainforest, are the Variable Screech-owl (*Otus atricapillus*), the Rusty-barred Owl (*Strix hylophila*), the Mottled and Black-and-white Owls, the Amazonian and Least Pygmy-owls and the Buff-fronted Owl. The Rufous-legged Owl and the closely related Chaco Owl inhabit dense subtropical and temperate forest in southern South America.

Extensive areas of rainforest are fast becoming rare in the Old World tropics, especially in South-east Asia and West Africa. Among the strigids largely confined to primary rainforest in Asia and western Indonesia are the White-fronted (*Otus sagittatus*) and Reddish Scops-owls (*Otus rufescens*), the Forest (*Bubo nipalensis*) and Barred Eagle-owls (*Bubo sumatranus*), and the Chestnut-backed Owlet (*Glaucidium castanonotum*). Similarly, the Ochre-bellied Hawk-owl (*Ninox ochracea*) is closely associated with rainforest in eastern Indonesia, as are the Jungle Hawk-owl (*Ninox theomacha*) and the Papuan Hawk-owl in New Guinea. In Africa, dense lowland rainforest occurs mostly in a band along the equator in the west-central part of the continent. Restricted to this endangered habitat are the Sandy Scops-owl (*Otus icterorhynchus*), the Maned Owl, Fraser's (*Bubo poensis*), Shelley's (*Bubo shelleyi*) and the Akun Eagle-owls (*Bubo leucostictus*), and the Red-chested (*Glaucidium tephronotum*), Sjöstedt's and the Albertine Owlets (*Glaucidium albertinum*). Little is known of the biology of most of these species owing to their patchy distribution and the difficulty of studying them in the dense forests they inhabit.

All four Australian strigids belong to the genus *Ninox*. The Rufous Owl is the second-largest member of *Ninox* and the least known of the four species. It occurs in three disjunct areas in northern Australia, in the lowlands of New Guinea, and on the Aru Islands. The two Queensland populations inhabit lush rain-

As it takes off from a post, a favourite lookout for many owl species, a Eurasian Eagle-owl reveals the long, feathered legs and toes typical of its genus. This species has a wide range in the Old World, extending right across Eurasia and into northern Africa. It occurs mostly in dry, rocky areas, forest and steppe, from lowlands to mountains, tending to avoid human contact.

[*Bubo bubo hispanus*, Torre Ponsa, Montgrí, Catalunya, Spain.
Photo: Ramon Mascort & Albert Burgas]



Although generally associated with forest and other types of woodland, the majority of owls by no means shun open spaces, especially if these provide a rich source of suitable food. Moreover, as demonstrated by this Eurasian Eagle-owl, even relatively secretive species will sometimes move from one favourable site to another by flying over open water, when they can then provide an unexpected sight for the vigilant observer.

[*Bubo bubo bubo*, Germany.
Photo: Dietmar Nill/
BBC Natural History Unit]



Owls in general are skilled and adept flyers, whether in open habitats or in closed forest and dense woodland. Flight is their main method of locomotion when approaching and capturing prey. Medium-sized and large species such as this male Ural Owl, a bird which prefers old-growth coniferous forest and edges, but also inhabits deciduous woodland in the south of its range, progress with a series of moderately slow flaps followed by a glide on outstretched wings.

The smaller species, typified by the tiny Austral Pygmy-owl of rather open forest and open country with trees and bushes, have a basically similar mode of progression, but the wingbeats are much more rapid and the glides are performed with the wings held closed against the body; over longer distances, this produces an undulating flight, not unlike that of a small woodpecker (Picidae).

[Above: *Strix uralensis*
liturata,
Häme, Finland.
Photo: Dick Forsman.

Below: *Glaucidium*
nanum,
Torres del Paine
National Park, Chile.
Photo: Günter Ziesler]





The eyes of owls are set well apart on the front of the face, which is very flat compared with that of most other avian families. This provides them with excellent depth of vision. Their eyes are not directed fully forwards, however, but diverge at an angle of approximately 50-55°, thus enhancing the total field of view. In order to increase the accuracy of depth perception provided by binocular vision, owls therefore bob the head and move it from side to side. This highly characteristic habit of strigids, frequently recorded in natural history films, enables them to measure distances with a remarkable degree of precision, an important advantage for open-country species such as the Short-eared Owl, which locate prey by sight as well as by sound.

[*Asio flammeus flammeus*, southern Alberta, Canada. Photo: D. Robert Franz/Planet Earth]

forest, whereas the population from the Northern Territory and adjacent Western Australia occurs in dense woodland bordering savanna. Wherever they occur in Australia, they have a penchant for living near watercourses. Although Rufous Owls are usually associated with lowland forest, a recent study by J. Kanowski showed that they are relatively common in highland forest at 800-1200 m in north-eastern Queensland. The aptly named Powerful Owl is the largest species of *Ninox* and occupies the most restricted range of the three better-known species in Australia. Powerful Owls occur in a narrow band along the Great Dividing Range in the south-eastern portion of the continent. The highest numbers are found on the coastal eastern side of the mountains, where they favour tall eucalypt forest on ridges and along valley bottoms. In undisturbed habitats, each pair requires 800-1000 ha of forest, and adjacent pairs may be separated by 5-20 km of unoccupied habitat. Territories are even larger in degraded habitats, and the birds are quite sensitive to habitat disturbance (see Status and Conservation). The medium-sized Barking Owl occurs in savanna, open woodland and forest edge in Australia and New Guinea. Its range in Australia forms a continuous ring extending around all but the southern and western edges of the continent, and includes a disjunct population south of Perth. The Southern Boobook is Australia's most abundant owl, occurring across the entire continent as well as in parts of New Guinea and the Lesser Sunda Islands. In his 1968 book *Nightwatchmen of Bush and Plain*, D. Fleay states that "Without a doubt, Australia's population of Boobook Owls runs into the millions for almost anywhere one camps at night...the leisurely sing-song 'morepork' call is as typical as the very gum trees." Southern Boobooks occupy virtually all major habitats within their vast range, including dense rainforest, eucalypt forest, savanna, farmland, suburbs and even desert. Although this species seldom occurs far from trees, in the more arid parts of its range it roosts in caves and beneath overhanging ledges on cliffs. In contrast to the other *Ninox* in Australia, Southern Boobooks feed mostly on insects. The diversity

of habitats in which they forage is reflected in the various substrates where they obtain their prey, which include the ground, tree trunks and the forest canopy, and they even capture prey in mid-air.

Unlike some sea-eagles (*Haliaeetus*) and coastal populations of Ospreys (*Pandion haliaetus*), no owl is restricted to salt water, although Blakiston's Eagle-owls and Northern Saw-whet Owls may forage in the intertidal zone. Owls in the genera *Ketupa* and *Scotopelia* feed mainly on aquatic organisms and seldom occur far from fresh water. The Brown Fish-owl inhabits a wide range of forest habitats near slow-moving streams, occurring from near sea-level on the southern coast of Asia to mountain forest in the interior of India and Pakistan. The Tawny Fish-owl is restricted to dense areas of forest along mountain streams, and it seems to prefer faster-moving water than the previous species. The Buffy Fish-owl is partial to coastal forest and mangroves in South-east Asia and adjacent Indonesia.

Blakiston's Eagle-owl, which is placed in the fish-owl genus *Ketupa* by some authorities, is the only piscivorous owl with a range that extends far beyond the tropics. Confined to the Russian Far East and Japan, it prefers dense, undisturbed forest near lakes or fast-flowing streams, and its numbers have declined in areas where this habitat has been destroyed (see Status and Conservation). The home range of a radio-tagged adult female on Hokkaido averaged about 3 km² during spring. Most of the radio locations occurred in mixed deciduous-coniferous forest, and the owl was never found more than 465 m from water.

All three species of fishing-owl inhabit riverine forest in Africa. Pel's Fishing-owl (*Scotopelia peli*) is the most widespread member of the genus and is patchily distributed throughout much of sub-Saharan Africa. Nowhere common, it occupies a greater range of elevations than the other fishing-owls. The Vermiculated Fishing-owl (*Scotopelia bowieri*) is relatively common along large rivers in the Congo basin, whereas the closely related Rufous Fishing-owl (*Scotopelia ussheri*) is quite rare and is known

only from Upper Guinea lowland forest and coastal mangroves from Guinea to Nigeria. The only other owls consistently associated with mangrove forest, at least in parts of their range, are the Pacific Screech-owl (*Otus cooperi*) of western Central America, the Palau Owl, and the Brown Hawk-owl of Asia and Indonesia. The last two species occupy a variety of forest types, in addition to mangrove, and the Palau Owl is the only living strigid that frequents Pacific atolls.

The Puerto Rican Screech-owl (*Otus nudipes*) is common in forested areas throughout the island of Puerto Rico and is rare on several of the Virgin Islands. Its distribution is thought to be limited by the availability of suitable forest habitat, and it has disappeared from at least two small islands in the Caribbean. K. L. Pardieck and associates recently assessed the influence of habitat fragmentation on this species by broadcasting vocalizations along roadsides in Puerto Rico. Owl responses to playbacks were quite high, averaging 0.96 to 1.1 responses per survey point, in both the unfragmented forest tracts (95% forest cover) and the fragmented tracts (36% forest). The results suggested that Puerto Rican Screech-owls can be reintroduced to islands where they have been extirpated, provided that suitable nesting cavities and food are available.

In contrast to many of the tropical species, most of the strigids that inhabit temperate forest in the Northern Hemisphere tend to be widespread, including several Holarctic species. The Eastern Screech-owl is a common inhabitant of deciduous forest throughout the eastern USA, and it is replaced in the western USA by the Western Screech-owl, which inhabits deciduous riparian forest. In parallel fashion, the Eurasian and Oriental Scops-owls replace one another in deciduous and mixed woodland from west to east across Eurasia. Likewise, the Barred Owl is quite common in North America and has an equally common counterpart in Eurasia, the Tawny Owl, both species frequenting deciduous, coniferous and mixed woodland. The Spotted Owl of the Pacific North-west of North America and the Ural Owl of northern Eurasia are tied to old-growth coniferous forest in much of their ranges; the southern race of the Spotted Owl occurs in wooded canyons amid arid habitats, whereas the Ural Owl inhabits deciduous woods in the southern part of its range. The Great Grey Owl, the

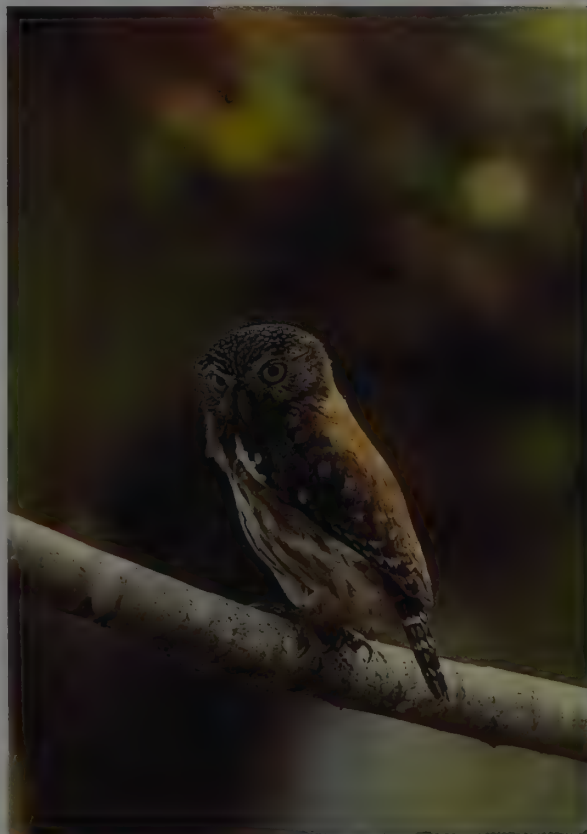
Northern Hawk-owl and the Boreal Owl occupy a band of boreal-forest habitat across Canada, Alaska and Eurasia. In the USA, Boreal Owls extend their range southwards along the Rocky Mountains, where they are restricted to spruce-fir forest at high elevations. Great Grey Owls extend south of the taiga into the Rocky Mountains and the Sierra Nevada range, where they occupy mixed forest of conifers and aspens (*Populus tremuloides*).

The Great Horned Owl probably occupies a wider range of habitats than any other species of owl. Occurring from the limits of the tree-line in Alaska and Canada south to southern parts of South America, Great Horned Owls are equally at home in stunted boreal forest, old-growth conifers, shrubland, grassland and treeless deserts. Indeed, one would be hard pressed to find a habitat in which they do not occur, especially in North America. The Great Horned Owl's success results in part from three factors. First, its huge size enables it to exploit a great diversity of prey types (see Food and Feeding); second, and related to the first factor, throughout most of its range it has no competitors of similar size and ferocity; and, last, it will nest almost anywhere where it can find suitable concealment, its nest-sites including cavities in cliffs or trees, broken-top snags, ledges on old buildings, stick nests built by hawks or corvids, and the ground. The breadth of habitats occupied by the Eurasian Eagle-owl is nearly as impressive. This species occurs across Eurasia, inhabiting mountain and lowland forest, steppe, farmland and rocky deserts. It tends to occur at lower densities than the Great Horned Owl and to shun areas frequented by humans, perhaps because it has experienced a longer period of human persecution than has its New World relative. Overall, the two species are similar in their use of habitat, and they play comparable roles in their respective ecological communities.

The arid thorn-scrub of sub-Saharan Africa supports a variety of owls that includes the African Scops-owl (*Otus senegalensis*), the Northern White-faced Owl, the Greyish and Verreaux's Eagle-owls (*Bubo lacteus*) and the Pearl-spotted Owlet. White-browed Hawk-owls occupy similar habitat in Madagascar. J. Mendelsohn's study of six sympatric owls, two tytonids and four strigids, in the Transvaal of South Africa revealed the influence of nest-sites and hunting behaviour on habitat

All owls have an extremely flexible neck, an ability necessitated by the fact that the eyes, unlike those of humans, are fixed in their orbits and can be moved by no more than 1° of arc; the owl can turn its head 270° to see sideways and behind it. In tandem with this, an intriguing plumage pattern shown by all the New World *Glaucidium* species, as well as some of the Old World ones, is the pair of "false eyes" on the back of the head. As demonstrated by this Least Pygmy-owl, these dark, normally pale-bordered patches bear a remarkable resemblance to an owl face and are thought to help these diurnal hunters to escape the attention of larger predators and smaller mobbing birds, by giving the impression that the owl is always watching them.

[*Glaucidium minutissimum*,
Pantanal of Mato Grosso,
Brazil.
Photos: Luiz Claudio Marigo]





The Strigidae family shows its greatest diversification in forested habitats of various types, which harbour as many as 95% of all the world's species of owl. Tropical forest is by far the most important, holding some 80% of the family's members. A significant number of these are more or less restricted to primary rainforest, as, for instance, is the Barred Eagle-owl of South-east Asia and the Greater Sunda, where this complex habitat is becoming increasingly fragmented and degraded.

[*Bubo sumatranus sumatranus*, Pasoh Forest Reserve, Peninsular Malaysia. Photo: Frank Lambert]

use in disturbed thorn-scrub. The study area of 6900 ha was composed of 72% cultivated land, 17% acacia woodland, 5% grassland, 5% roads and 1% farmyards, and was highly altered by humans and livestock. Among the strigids, Spotted Eagle-owls and Pearl-spotted Owlets tended to nest and roost in exotic trees near homesteads, whereas Southern White-faced Owls were associated with native acacias. Marsh Owls, on the other hand, nested on the ground beneath isolated clumps of grass or small shrubs, and roosted communally in open acacia woodland. Because they hunted exclusively from perches, Southern White-faced Owls, Spotted Eagle-owls and Pearl-spotted Owlets were absent from treeless habitats, whereas Marsh Owls were less restricted in their use of hunting habitats. A high density of prey facilitated the co-existence of many individual owls in the area.

The arid scrubland of South America is inhabited by the race *pacificus* of the Peruvian Screech-owl and by the Austral and the Ferruginous Pygmy-owls. The last two species also occur in habitats other than scrub, including open deciduous forest and even city parks. Indeed, the Ferruginous Pygmy-owl has the largest geographical range of any *Glaucidium* in the New World, occupying deserts, savanna and semi-arid woodland from South America north into Texas and Arizona in the USA.

Only six strigids can truly be called non-forest species. These are the Snowy, Hume's, Little, Burrowing, Short-eared and Marsh Owls. The Snowy Owl breeds in Arctic tundra characterized by rolling terrain with high spots or rises that are used for nest-sites and as vantage points. Hume's Owl is a "wood-owl" that does not live in woodland; it frequents desert gorges, canyons and palm groves, and often occurs near water. The Little Owl inhabits open country throughout the middle latitudes of the Palearctic, favouring shrub-steppe and semi-desert. It is thought that it did not colonize central and western Europe until lowland forest areas were cleared in the Middle Ages. This species may have occurred in Britain during the Pleistocene; it was re-established there in the late nineteenth century after several unsuccessful attempts at reintroduction, and there may currently be as many as 10,000 pairs in Britain, where it frequents farmland and pastures and is often associated with human habi-

tation. In western North America, the Burrowing Owl occurs in grassland, shrubland and deserts, so long as these habitats contain suitable burrows for nest-sites (see Breeding); it has also adapted to civilization, and routinely nests at such places as golf courses, airports and college campuses and in other open habitats created by humans; in South America, it occupies savanna and alpine grassland, as well as various desert-like habitats. The Short-eared Owl tends to be nomadic, wandering from place to place in search of concentrations of prey. Regardless of the time of year, and throughout its vast geographical range, this owl inhabits open country of one sort or another; grassland, marshes, shrubland and tundra are used for breeding, provided that adequate cover, usually in the form of tall grasses, exists to conceal the female on the nest. The Short-eared Owl has colonized remote oceanic outposts such as the Hawaiian and Galapagos Archipelagos; in Hawaii it occupies open shrubland and pastures, and in the Galapagos it occurs in upland *pampas* but also forages at seabird colonies along the coast. The Marsh Owl is more or less an ecological equivalent of the Short-eared Owl in Africa, where it inhabits marshes, grassland and savanna south of the Sahara Desert and in Madagascar. Like the Short-eared, the Marsh Owl tends to be nomadic in response to fluctuating prey numbers.

Two species occupy a mix of open and sparsely forested habitats. The Elf Owl frequents deserts, especially cactus desert, and other treeless habitats in the North American South-west, but also occurs in riparian woodland and open forest on slopes above deserts. The Northern Long-eared Owl inhabits much the same range as the Short-eared Owl, but does not occur in South America or on oceanic islands. In western North America, the Northern Long-eared is most abundant in desert shrubland and grassland, where it nests and roosts in dense thickets of deciduous vegetation adjacent to open areas, using the latter for hunting. Especially in eastern North America, the Northern Long-eared Owl roosts in conifer groves during the winter, and it occasionally nests in open conifer forest throughout its North American breeding range. In Eurasia, this species occupies wooded patches in a variety of open and semi-open habitats,

Owls range across a broad spectrum of climatic regions, from the very cold

Arctic to the hot, arid deserts of the tropics and subtropics. This Northern Hawk-owl gained some respite from the severity of the far northern winter by taking up temporary residence in the photographer's garden, where it remained for four months, presumably taking advantage of an improved or more easily accessible food supply.

At the other extreme, those species inhabiting the vast arid wildernesses of the desert would seem unlikely to find similar human assistance.

The race desertorum of the Pharaoh Eagle-owl, here photographed in the harsh desertic conditions of the southern edge of the Sahara, has to eke out an existence by catching any small rodents that it comes across.

Nevertheless, in these two contrasting environments, the owls manage to survive well, being supremely adapted to the respective habitats in which they live.

[Above: *Surnia ulula ulula*, south Finland.
Photo: Dick Forsman.

Below: *Bubo ascalaphus desertorum*,
Ténéré Desert, Niger.
Photo: Alain Dragesco/
Planet Earth]





While Hume's Owl is frequently associated with dry, rocky desert wadis and gorges and similar open habitats, it can often be seen also in and around palm groves. This attractive owl occurs near freshwater springs, too, and even on the edge of human settlements, but tends in general to avoid human contact. In sharp contrast to its darker northern relative the Tawny Owl (*Strix aluco*), however, which is strictly a forest and woodland bird, Hume's Owl is one of the mere half-dozen strigids that can be accurately described as a non-forest species.

[*Strix butleri*, near Dead Sea, Israel.
Photo: Eric & David Hosking/FLPA]

and is perhaps more of a forest owl than in North America; outside the breeding season, however, it can also be found in open, treeless country such as moorland and steppe.

Most strigids are non-migratory, but those that do migrate (see Movements) tend to winter in habitats that have the same general structure as those used during the breeding season. For example, Eurasian Scops-owls breed in open forest in western Europe and migrate to central Africa, where they winter in open forest and savanna. In the northern Rocky Mountains, Flammulated Owls migrate from their breeding sites in montane pine forest, presumably to winter in the extensive areas of pine forest in Mexico. Snowy Owls that move south for the winter occupy grassland, farmland, marshes and dunes, habitats that are structurally similar to tundra. Burrowing Owls migrate from the northern part of their range in western North America to winter in the Southern Great Plains, where they exploit habitats that are very similar to those occupied on the breeding grounds.

Some owls do, however, undergo seasonal shifts in habitat. Several Northern Long-eared Owls radio-tagged by H. Ulmschneider in the shrub-steppe desert of the Snake River Birds of Prey Area, in south-western Idaho, left their breeding territories soon after the young fledged to spend the summer in open conifer forest in the foothills north of the Snake River Plain. In the same study area, in years when small mammals are abundant, Northern Saw-whet Owls, which normally nest in moist coniferous forest, breed in nestboxes in deciduous riparian thickets in the desert. Before these nestboxes were available, this species was not known to breed in shrub-steppe deserts, although it was relatively common there during migration and in winter.

Owls generally are not considered to be birds of high mountains, and most species live at elevations between sea-level and 2000 m. Several species ascend to 2500 m, however, and a few can be found at much higher elevations than that. For example, Eurasian Eagle-owls inhabit pastures at up to 4700 m in Tibet, Andean Pygmy-owls and Rufous-banded Owls occupy forest at 3700 m or above in the Andes, Burrowing Owls live on alpine plateaux above 4000 m in South America, and African Long-eared Owls have been observed at 3500 m in Kenya and at nearly 4000 m in Ethiopia.

General Habits

Nocturnal owls spend the daylight hours perched quietly in concealed sites, such as amid the foliage and branches of a tree, in a recess on a cliff, or inside a cavity. Cryptic plumage serves to hide owls from daytime predators and mobbers, not to conceal them from potential prey. Many species are considered to be "tame" because they often allow close approach before taking flight. It is true that some owls are indeed remarkably tame, such as those Arctic and boreal species that seldom see human beings until a crash in prey numbers drives them south, or to lower elevations, for the winter, when they may end up perched along a busy road, seemingly oblivious to the cars and the people passing below them. For owls that routinely encounter humans, however, so-called tameness is a part of their behavioural repertoire designed to avoid detection.

Take, for example, the typical reaction of a Northern Long-eared Owl to a human being, a response that would apply equally well to other similar-sized species. In the absence of disturbance, the owl perches in a "relaxed" position on a limb, concealed from view by the trunk and surrounding branches. At the approach of a human, the owl stretches out vertically and draws its contour feathers against its body in what can be described only as an attempt to appear as thin as possible; the eyes are partially open, and the ear-tufts are erect. If the person does not make eye contact with the owl, the owl will retain its position and posture as the intruder walks past it, sometimes as close as half a metre. If eye contact occurs, however, the owl ceases its "concealing" posture, opens its eyes wide, and flies away. It may fly to several different perches if the human being continues pursuit, but it will not adopt the concealing pose again, nor will it remain perched as the human approaches. On the basis of this scenario, one may infer that owls routinely respond to a terrestrial predator by remaining still if the predator passes by without knowing that the owl is present.

Smaller species, such as the Eurasian and Northern Pygmy-owls, the Boreal Owl and the Northern Saw-whet Owl, exhibit a variation of the aforementioned pose. In this case, the eyes are suddenly opened wide, the whitish feathers between the eyes are

Of all the world's owls, the Great Horned Owl must surely occupy the widest range of habitats. It occurs throughout most of the Americas, from the limits of the tree-line in the north Nearctic south to the southern parts of South America. Within many parts of this huge range it is likely to be found in forested areas of most types, but it can also be met with in grassland, shrubland and entirely treeless habitats. It is equally at home in rocky areas and places with steep gorges, or around the stone walls of canyons, as it is in the comparatively "softer" habitat of old-growth conifer stands. This highly successful species has been able to exploit virtually all available habitats because it has no major competitors, it takes a very wide range of prey, and it will accept a considerably broad spectrum of nesting sites, including cliff cavities and suitable ledges on rock faces and old buildings, so long as these provide sufficient concealment. Unlike its Old World counterpart, the Eurasian Eagle-owl (*Bubo bubo*), the Great Horned Owl does not shun areas frequented by human beings; as a consequence, it is rather better known to many people than is the latter species.

[*Bubo virginianus*
pallascens,
Antelope Canyon,
Arizona, USA.
Photo: John Netherton/
Oxford Scientific Films]



erected, the crown feathers above the eyes are raised to resemble "ear-tufts", and one wing is elevated to the level of the bill like a vampire raising its cape to its face! Although this posture is termed a "concealing pose" by some authors, S. Bondrup-Nielsen pointed out that this behaviour is revealing rather than concealing, because the abrupt movements made while opening the eyes and raising the wing, and the accentuation of the white patches around the eyes, would be likely to draw the attention of a predator. Bondrup-Nielsen suggested that the pose be termed an "erect posture" to avoid confusion with true concealing behaviour. Subsequent study of a Northern Saw-whet Owl by S. G. Sealy and K. A. Hobson supported the revealing function of the erect posture, and these researchers suggested that the posture is a fright response to disturbance, or that it perhaps serves to threaten a potential predator.

Mobbing is a type of anti-predator behaviour in which individuals approach a potential enemy and perform conspicuous calls and visual displays; the predator may or may not be struck during the mobbing event. Owls are popular targets for mobbing birds, but most studies of mobbing have focused on the mobbers rather than the predators. One exception is the recent study by C. R. Pavey and A. K. Smyth on how mobbing influenced the roosting behaviour of a family of Powerful Owls. Pavey and Smith observed 35 cases of mobbing involving seven species of mobbers; ten mobbing bouts were directed at the male owl, 17 at the female, and eight against the three young owls. Mobbers ranged in size from the Grey Fantail (*Rhipidura fuliginosa*) of 8 g to the Pied Currawong (*Strepera graculina*) of 320 g, which translated to 4-26% of the mass range of the owls. Of the 33 mobbings observed in sufficient detail, seven produced no apparent response by the owl, 19 elicited a vocal response, and in seven cases the owl moved its perch, sometimes with the mobber in hot pursuit. Half of the 229 recorded owl roosting sites were in rainforest and half were in open forest, even though rainforest made up only 12% of the study area. Mobbing occurred more frequently when the owls roosted in open forest than when they used rainforest, with 77% of mobbing events in the former and 23% in the latter. This suggests that the owls selectively roosted in rainforest in order to avoid being mobbed.

Many owls are aggressive near their nests, especially after the chicks have hatched. Nesting Great Grey Owls sometimes attack black bears (*Ursus americanus*), and they routinely drive off Northern Goshawks (*Accipiter gentilis*) that enter the nest area. In addition, larger species such as the Great Horned Owl, the Eurasian and Verreaux's Eagle-owls, and the Snowy, Ural and Great Grey Owls often strike human beings. Indeed, the Ural Owl in northern Scandinavia is renowned for its readiness to attack anybody who is rash enough to approach its nest and young, and it will go for the eyes of the intruder; despite its "good looks", it can be a very dangerous bird if approached at the wrong time of the year! Medium-sized species such as the Tawny Owl, African Wood-owl, Northern Hawk-owl and Northern Long-eared Owl, and even small species such as the Eastern Screech-owl and Eurasian Pygmy-owl, also strike humans on occasion. Species not known to strike human beings will nonetheless swoop at them when defending the nest. It seems likely that these species would vigorously attack smaller predators that are less formidable than humans. In many strigid species, both sexes defend the nest, but the female is usually the more aggressive sex (see Breeding).

In a typical threat posture, an owl crouches with its head lowered, its wings drooped, and the body feathers ruffled so as to increase its apparent size. The adults and young of many species also adopt a spread-wing posture in which the wings are turned vertically and fanned out above and to the sides of the head, again with the effect of increasing the apparent size of the individual. Most species utter a variety of vocalizations and clack their bills during these aggressive displays. The wing-clapping display of courting Northern Long-eared, Short-eared and Marsh Owls (see Breeding) is used also in aggressive interactions with predators and conspecifics.

A suitable roosting site satisfies several different functions, including concealment from predators and protection from harsh environmental conditions. Many cavity-nesting species also roost in cavities, but important exceptions exist. G. A. Sonerud's study of three hole-nesting owl species in Norway determined how the risk of nest predation influences behaviour during incubation, and his results can be extended to roosting behaviour. Nesting

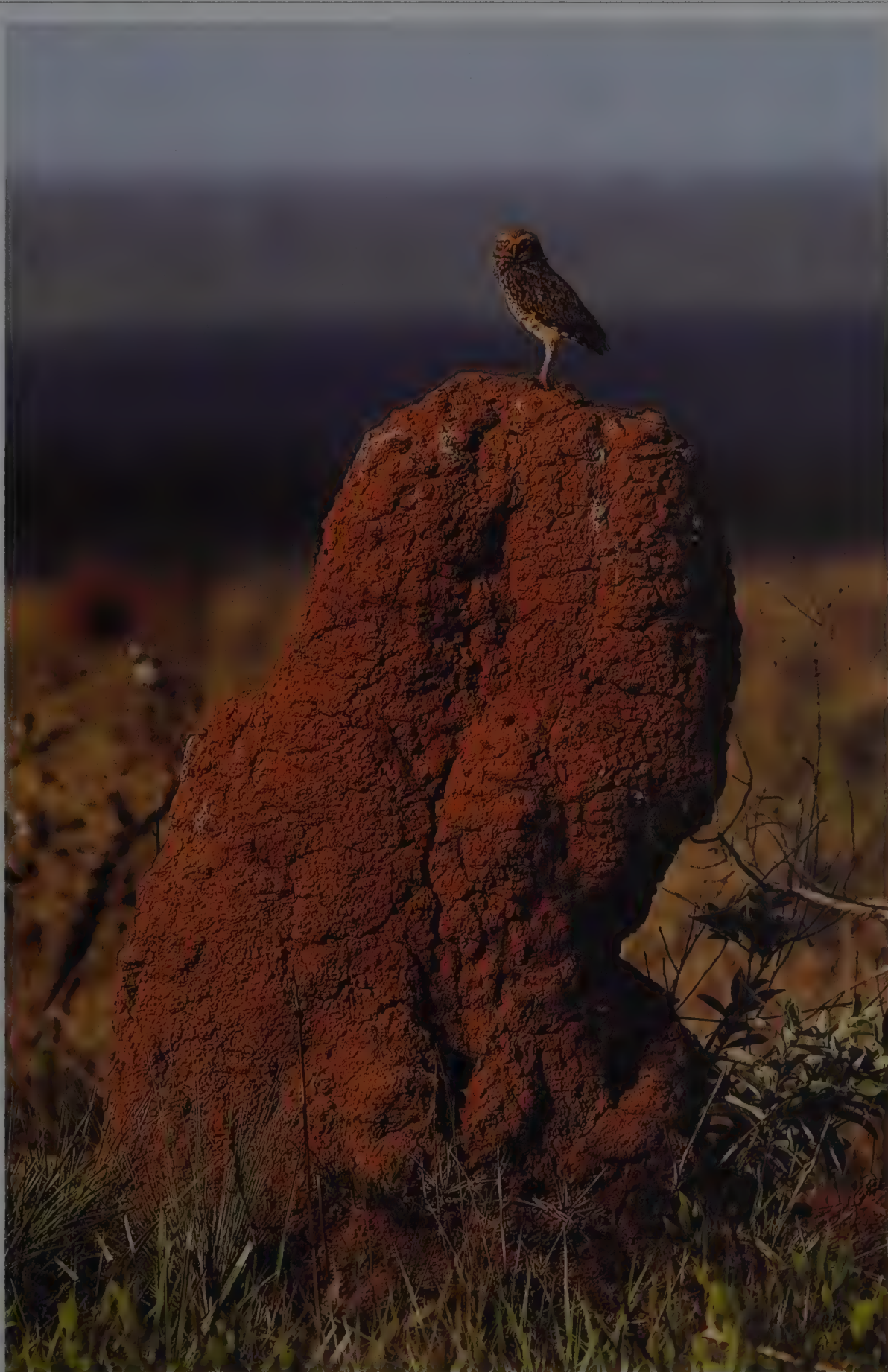


Since they feed largely on a diet of aquatic organisms, the Asian fish-owls of the genus *Ketupa* require the proximity of fresh water. The Brown Fish-owl is a typical example. This magnificent species inhabits various types of forest, especially dry forest, with slow-flowing streams; in such places it prefers large, old trees, often on steep banks, from where it can drop down to catch fish and other items.

[*Ketupa zeylonensis* leschenault, Ranthambore National Park, India. Photo: Anup & Manoj Shah/Animals Animals]

A once familiar sight in parts of western North America is that of a Burrowing Owl perched on a lookout in open grassland and desert country. This species, which has declined greatly in the north of its range, remains a reasonably common bird in South America, where it occupies similar habitats and is a characteristic bird of savanna, alpine grassland and desert-like areas with short, rather sparse vegetation. It can often be seen keeping watch from an elevated site such as a termite mound, as is this individual, photographed in the cerrado region of south-central Brazil. For nesting, these owls require underground burrows, especially those dug by prairie-dogs (*Cynomys*), so the substrate of their habitat needs to be reasonably soft. With the widespread loss of natural grassland, particularly in the USA, Burrowing Owls have adapted to man-altered environments and now frequent such places as grassy airfields, golf courses and college campuses.

[*Athene cunicularia*
grallaria,
Emas National Park,
Goiás, Brazil.
Photo: Günter Ziesler]





cavities required by Northern Hawk-owls and Boreal Owls were large enough for Eurasian pine martens (*Martes martes*) to enter, but those used by Eurasian Pygmy-owls were not. When Sonerud scratched on the trunks of nest trees to simulate an approaching predator, incubating females of the first two species appeared at the nest-hole immediately, ready to take flight, whereas female Eurasian Pygmy-owls did not. The results indicate that vulnerability to predation influences the behavioural responses of these species during the incubation period.

Studies in North America and Eurasia have shown that male Northern Hawk-owls and Boreal Owls hardly ever roost in cavities, and that females use cavities only during the incubation and brood-rearing stages. Similarly, Flammulated Owls and Northern Saw-whet Owls often nest in habitats used by American pine martens (*Martes americana*), but males do not roost in cavities and females use them only during the nesting season. Although Flammulated Owls can fit into holes that are too small for martens to enter, they often use Pileated Woodpecker (*Dryocopus pileatus*) cavities that are large enough to admit martens. In contrast, Western and Eastern Screech-owls live in habitats where martens typically do not occur, and males and females of both species routinely roost in cavities throughout much of the year. In agreement with Sonerud's Norwegian results, experiments have revealed that female Flammulated and Northern Saw-whet Owls appear at the cavity entrance immediately if someone scratches the base of the nest tree, whereas incubating and roosting screech-owls of both species seldom react to such disturbance.

Independent of predator avoidance, an obvious benefit of roosting in a cavity is the favourable micro-climate it provides. Western Screech-owls in south-western Idaho almost never roost in nestboxes during the hot summer months, but use them regularly from September through to March. Similarly, Eastern Screech-owls in central Texas show a preference for roosting in boxes or natural cavities during the winter and spring months, but not during summer. Non-enclosed roost-sites may function to provide a cool micro-climate. During the heat of the summer, Spotted Owls in California select shaded roosts that are up to 6°C cooler than exposed sites; moreover, they switch roost-sites during the day in response to increases in ambient temperature and exposure to direct sunlight.

Body temperatures of strigids generally range between 38°C and 41°C. Compared with most other groups of birds, owls tend to have a lower basal metabolic rate, less variation in the daily cycle of body temperature, and denser plumage. On balance, they have more trouble keeping cool than keeping warm. Indeed, J. D. Ligon showed that body temperatures of 42.3 to 44.3°C are lethal to Elf Owls and Northern Saw-whet Owls in as little as 10-20 minutes. As temperature increases beyond the upper limit of the thermoneutral zone, owls respond by reducing their activity, compressing their contour

Old trees and dead wood are important elements of the forest ecosystem, and therefore in the habitat of most forest-dwelling owls. Strigids do not build their own nests, but in most cases rely instead on the presence of natural cavities or of holes excavated by other birds, these hollows being found almost exclusively in old or dead wood. It is consequently essential that sufficient old timber remains to supply suitable sites for nesting and roosting by such species as the White-browed Hawk-owl.

[*Ninox supercilialis*, Berenty Private Reserve, Madagascar.
Photo: Jordi Sargatal/Lynx Edicions]



One of the ways in which the numerous strigids inhabiting forest avoid direct competition is by exploiting different strata of the habitat, or by hunting at different times of the day. The Collared Owllet uses open edges and scrub, where it tends to operate at lower levels; it is active at all hours, frequently foraging during daylight. This individual was photographed in the middle of the afternoon, at a perch about 4 m above ground. The comparatively long tail of this genus is also shown to advantage here.

[*Glaucidium brodiei*, brodiei, Khao Yai National Park, Thailand.
Photo: Bernard Van Elegem]

The typical threat posture adopted by many strigids is designed to make the owl appear bigger than it really is, and this applies even to the large species such as the Spotted Eagle-owl. The owl assumes a crouched stance, with head lowered, wings drooped and feathers ruffled, thereby increasing its apparent size quite considerably. At times it may raise the wings and turn them forwards to face the source of the danger, making intermittent lunging movements.

[*Bubo africanus africanus*,
Helderberg Nature
Reserve, South Africa.
Photo: Peter Steyn/Ardea]



feathers against the body, which reduces insulation, and holding their wings out from the body. If heat stress continues, owls use evaporative cooling by panting and gular-fluttering, the latter being accomplished by rapid vibration of the hyoid apparatus in the throat. Rates of gular-fluttering under heat stress were found to be 215-540 flutters per minute for Western Screech-owls, 176-523 for Elf Owls, 150-386 for Whiskered Screech-owls (*Otus trichopsis*), and 109-435 for Northern Saw-whet Owls. Panting rates for Whiskered Screech-owls and Elf Owls were 68-128 and 135-160, respectively.

Although all strigids are nocturnal to some extent, activity times vary considerably, both within and among species. By and large, species in the genera *Otus*, *Bubo*, *Strix*, *Jubula*, *Lophotrix*, *Aegolius*, *Ninox*, *Pseudoscops* and *Nesasio* are nocturnal. Eurasian Scops-owls and Eastern Screech-owls may be crepuscular or occasionally diurnal, especially during the breeding season, and Pallid Scops-owls (*Otus brucei*) have also been observed hunting by day. Spotted and Dusky Eagle-owls (*Bubo coromandus*) are crepuscular-diurnal, and Great Horned Owls and Verreaux's and Rock Eagle-owls will kill prey animals that wander under their daytime roosts. Among species of *Strix*, Spotted and Great Grey Owls hunt during the day when provisioning their young, and the latter species is also partly diurnal in winter. The four species of *Athene* are mostly nocturnal, but in much of their range Little Owls are active at any hour of the day, especially at twilight, and have been seen feeding young during the day in Morocco and Spain. Burrowing Owls commonly perch outside their burrows during the day, and for many years biologists thought that they were diurnal; night-time observations based on radio-telemetry and night-vision scopes, however, have proven that the birds are decidedly nocturnal hunters. Five of the seven species of *Asio* are nocturnal, but two, the Short-eared and Marsh Owls, hunt by day and night throughout the year. Boreal Owls and Northern Long-eared Owls are nocturnal except at the northern edge of their ranges, where they have no option but to hunt in daylight during the summer. Similarly, Snowy Owls and North-

ern Hawk-owls have to forage in the 24-hour daylight of the Arctic summer, but they hunt during the day and night in winter.

In many parts of the world, an owl seen hunting during the day is likely to be a pygmy-owl or owlet, and the genus includes some of the least nocturnal of the strigids. Indeed, on every continent in which they occur, at least three species of *Glaucidium* are conspicuous daytime hunters: the Eurasian Pygmy-owl, Collared Owlet (*Glaucidium brodiei*), Asian Barred Owlet and Jungle Owlet (*Glaucidium radiatum*) in Eurasia; the Pearl-spotted, Red-chested and African Barred Owlets in Africa; the Andean, Least and Austral Pygmy-owls in South America; and the Northern, Mountain and Ferruginous Pygmy-owls in North America.

Several nocturnal species have been subjected to all-night observations in an attempt to determine the temporal distribution of their foraging activity. A Flammulated Owl nest monitored in Idaho revealed that foraging activity began 10-30 minutes after sunset and continued until an hour before sunrise; activity peaked early in the evening and again just before sunrise, and there was no evidence that the owls foraged during the day. Four Tawny Fish-owls radio-tagged in Taiwan returned to their day roosts an average of 8-2 minutes before sunrise and left the roosts to resume foraging an average of 5-8 minutes before sunset; the owls were active throughout the night, but foraging activity peaked in the first hour after sunset. Similarly, radio-tagged Tawny Owls foraged throughout the night in Britain, but their activity was highest in the first hour or two after dusk. Other studies have shown that Tawny Owls occasionally hunt in daylight, especially when provisioning their young.

Radio-tagged Northern Long-eared Owls tracked in southeastern Idaho during the breeding season were active only at night. Presumed hunting activity was lowest in the first two hours after dusk and in the last hour before sunrise, and such weather factors as wind speed, precipitation and cloud cover had little effect on activity. Four more radio-tagged Northern Long-eared Owls, tracked during autumn and winter in the Netherlands, reduced their flight activity during periods of sleet. Independent



The owls are recognized as serious predators by all other bird species. As a result, they are subjected to constant attacks at all times of the year. Even owls as big as a female Snowy Owl are not immune from such attacks. On their breeding grounds in the Arctic, these huge birds are continually harried by other breeding birds, notably Long-tailed Skuas (*Stercorarius longicaudus*), notorious mobbers of all predators, including humans. Despite being dive-bombed, and even struck, by the skuas, the owl appears unworried by such harassment.

[*Nyctea scandiaca*, Greenland National Park, Greenland.
Photo: Jean-Louis Klein & Marie Luc Hubert/Bios]

of weather conditions, flight activity peaked five to six times each night, perhaps reflecting the cycle of above-ground activity by voles. Roughly half of the foraging flights lasted less than five minutes, and only 10% of the flights exceeded ten minutes. The owls spent a median of 158 minutes in flight per night, which translated to about 20% of the time that they were active.

Unmarked Snowy Owls observed from December to February in Alberta, Canada, spent 98% of the daylight hours perched. Their hunting activity, in the form of perch changes and flights, peaked just after sunrise and just before sunset, and most attempts at prey capture occurred in the late afternoon. Because the observed rates of prey capture failed to balance the estimated daily energy budget, the researchers assumed that the owls carried out a considerable amount of hunting at night.

Most owls are solitary or occur in mated pairs. Non-migratory cavity-nesters tend to be highly territorial all year round, in order to maintain possession of scarce nesting sites. In species with permanent pair-bonds, both sexes vocalize to advertise their presence and keep out conspecifics. When referring to data on spatial use, it is important to keep in mind the distinction between a "home range" and a "territory", the former being the total area occupied by an individual or pair, and the latter being the area that is defended against conspecifics. Often, researchers who follow radio-tagged individuals are able to estimate home-range size but cannot say for certain how large an area is defended, especially if "territories" are not contiguous among adjacent breeding pairs.

Eurasian Scops-owls, which are almost wholly migratory in most of their range, apparently defend only a small territory around the nest; up to five nests have been reported in an area of only 0.6 ha, with the closest nests only 10 m apart! Home-range size varies within and among species and tends to increase with increasing body size. Accordingly, average home-range sizes of five non-migratory species in Europe, in increasing order of body size, are: 0.4-1.25 km² for Eurasian Pygmy-owls (50-80 g); 0.3-0.4 km² for Little Owls (150-200 g); 0.2-0.6 km² for Tawny Owls

(400-600 g); 4-5 km² for Ural Owls (600-1200 g); and 12-20 km² for Eurasian Eagle-owls (1500-4000 g). The relatively large home range of Eurasian Pygmy-owls perhaps reflects the preponderance of birds in their diet. Indeed, home-range size generally decreases as prey density increases. For example, breeding Snowy Owls defend 1-4 km² of tundra during high lemming years and 8-10 km² during lows in the lemming cycle. In an especially poor lemming year, a non-breeding pair may occupy a home range of 20 km². Similarly, the average territory size of Short-eared Owls over a three-year period in Scotland varied from 42 ha to 112 ha and was negatively correlated with vole abundance. Habitat characteristics may also influence territory size, independent of food availability. For instance, the territory size of Tawny Owls is smaller in woodland than in more open habitats, and the amount of woodland within a territory is negatively correlated with territory size.

Using radio-telemetry in combination with playback of vocalizations, P. Finck determined how average territory size varied throughout the year in a population of Little Owls in Germany. The largest territories, covering 28.1 ha, were defended during the courtship period in March and April, and males decreased the size of their territories to 12.6 ha during brood-rearing in May and June. Territories were smallest, at only 1.6 ha, in late summer, when broods were out of the nest but still being fed by their parents. Territory size increased to 9.5 ha during September and October, which corresponded to the post-fledging dispersal period, and increased further from November to February, when it extended over 19.8 ha. Despite the increase in defended area from autumn to winter, response to playbacks indicated that males were less aggressive in winter than during the spring courtship period. Aggressive behaviour ceased on days with cold temperatures and snow cover, suggesting that, in terms of energy expenditure, foraging then took precedence over territorial behaviour.

Only four species of strigids can genuinely be considered to be social. These are the Burrowing, Northern Long-eared, Short-

eared and Marsh Owls. No species, however, is truly colonial. Burrowing Owls sometimes nest in loose colonies, with densities of active burrows approaching 16 per ha in the best of conditions. Nearest-neighbour distances in these situations may be as little as 14 m. The owls do not seem to defend territories for hunting or nesting, and overt aggression is seldom observed except in extreme cases when an individual disturbed by humans attempts to enter a neighbour's burrow. Northern Long-eared Owls also are facultatively colonial, with nesting aggregations occurring in isolated tree groves during years of abundant prey. In Israel, as many as twelve nests have been recorded in a colony, with inter-nest distances of no more than 10 m; in the western USA, six Northern Long-eared Owl nests may be active simultaneously in an area of less than 2 ha, the closest nests being only 14 m apart. Like Burrowing Owls, Northern Long-eared Owls do not defend a nesting territory, and radio-telemetry studies have shown that close-nesting pairs overlap widely in their use of hunting areas. Marsh Owls in Africa also nest in loose aggregations, although not to the same extent as Northern Long-eared Owls, the closest nests being about 75 m apart. Unlike the Northern Long-eared, Marsh Owls are known to defend territories against conspecifics. Also worthy of mention with regard to sociality are Great Grey Owls, which are sometimes tolerant of conspecifics outside the pair-bond: as many as four adult males and their fledged young have been observed hunting in the same field in Manitoba, Canada. The extent to which Great Grey Owls defend hunting territories against members of their own species is unknown.

Burrowing Owls and Northern Long-eared Owls are not colonial nesters in the true sense, because they do not congregate together in the way that obligate colony nesters such as, for example, many seabirds, herons and Arctic geese do. For either of these two owl species, one gets the impression that adjacent pairs could be removed from a nesting aggregation without any effect on the remaining pair or pairs, which is in marked contrast to a colonial species, which settles preferentially near conspecifics. The adaptive significance, if any, of semi-colonial nesting in Burrowing and Northern Long-eared Owls is not known. Quite possibly, the birds may be drawn to areas with suitable nesting sites and adequate food resources, where they congregate passively because they are not territorial. Close-nesting individuals of both species do, however, participate in group defence against predators, and the success in deterring a formidable predator undoubtedly is higher for a group than for an individual, raising the possibility that group-nesting is adaptive.

Sociality outside the breeding season is well developed in Northern Long-eared, Short-eared and Marsh Owls, each of which roosts communally in winter. Such roosts often contain more than 20 individuals, although smaller and notably larger numbers are common; some Short-eared Owl roosts may hold more than 100 individuals. Communal roosts of Northern Long-eared Owls occur in dense thickets of deciduous trees in the western USA and Europe and in conifer groves in the eastern USA, whereas those of Short-eared and Marsh Owls are typically on the ground amid tall grasses and weeds. Small numbers of Short-eared Owls occasionally roost with Northern Long-eared Owls in trees. Hunting areas around communal roosts overlap widely, and agonistic interactions typically are confined to cases where the paths of two courting birds bring them into close contact with one another.

Owls exhibit the typical range of comfort movements and maintenance behaviour observed in other groups of birds. Sunning, bathing, dusting, preening, scratching (under as opposed to over the wing), and stretching have been described for several owl species, and no doubt occur in all of them. To date, anting behaviour is unknown in owls.

Allopreening, in which one individual preens another, usually its mate, has been described for at least 17 species of Strigidae in the wild. These are the Eurasian Scops-owl, Western and Eastern Screech-owls, Great Horned Owl, Eurasian and Verreaux's Eagle-owls, Tawny, Spotted, Barred, Ural and Great Grey Owls, Northern Hawk-owl, Eurasian Pygmy-owl, Little and Burrowing Owls, Powerful Owl and Northern Long-eared Owl. The behaviour often occurs between pair-members and is also observed, though less frequently, among siblings or between adults and their young. Researchers have suggested that allopreening is a means of reducing or redirecting aggression, but in owls the behaviour is peaceful and without aggression. Whatever its origin or function, allopreening in owls appears to be a non-aggressive, ritualized type of behaviour, and it is probably indulged in by many more species than the 17 listed above.

Voice

Voice plays an important role in the lives of owls, which is not surprising for a largely nocturnal group that cannot easily communicate through visual displays. The loud vocalizations of many species have given them their names, both common and scientific. For example, the Eurasian Eagle-owl is known as "Uhu" in

Whenever they appear during the daytime, owls are likely to be mobbed by small birds. This anti-predator strategy is practised by a wide range of avian species throughout the world, and involves loud calls and a variety of displays; sometimes the potential enemy is struck by the mobbing birds. The same treatment is handed out to owls that are discovered at their daytime roost. This White-browed Hawk-owl may appear fairly oblivious to the attentions of a male Madagascar Paradise-flycatcher (*Terpsiphone mutata*), but it is not uncommon for the predator to be forced to move to a different perch to escape the mobbing.

[*Ninox superciliosus*,
Berenty Private Reserve,
Madagascar.
Photos: Roland Seitre/
Bios]



Germany, "Huuhkaja" in Finland and "Buho" in Spain; all are names that refer to its booming two-noted call. The boobook owls of Australasia comprise another group with onomatopoeic etymology. The Spectacled Owl is known as "Oropopo" in Costa Rica, a good imitation of its primary call. In English, the screech-owls are obviously named for one of their calls, as are the saw-whet owls, which are named after a call that supposedly sounds like a saw being sharpened.

Because strigid vocalizations are innate, rather than learned, they provide valuable clues for species limits and phylogenies in a family where plumage and other morphological characters are very similar among species (see Systematics). For instance, vocal differences enable two groups to be distinguished within the large genus *Otus*: the Afro-Eurasian scops-owls, with a single, simple primary song, and the New World screech-owls, which have a relatively complex two-part primary song. The two species of white-faced owls of Africa were formerly considered scops-owls, but their complex trilled songs are more similar to those of North American screech-owls; further investigation has shown that they do not appear to belong to *Otus* at all, and they are now placed in their own genus, *Ptilopsis*. Vocal characters have been used many times in recent years to clarify species limits in *Otus* and *Glaucidium*. For instance, the sedentary African Scops-owl was once considered conspecific with the migratory Eurasian Scops-owl because of morphological similarities between the two; their very different songs, however, resulted in the two species being split.

Hybrids between the Barred Owl and the Spotted Owl give unique location calls that are intermediate between the typical calls of the two species, but some of their calls may end in the vibrant "hoo-aww" note characteristic of the Barred Owl's song.

As in other bird groups, owls use vocalizations in many contexts: to attract a mate; advertise a territory; maintain contact between pair-members; indicate alarm; defend the nest or young; and beg for food. The nocturnal habits of owls, however, make it difficult to study these contexts. In many cases, the sex or even

the species giving the vocalization is not known. This is especially true for vocalizations other than the primary songs used to attract a mate or proclaim a territory. Akun Eagle-owls, for instance, emit a high-pitched wailing "heeuuuw" call that is probably used for solicitation, but whether it is given by females, by young or by both is unknown.

Species that are year-round residents on their territories tend to increase the frequency of primary vocalizations when their young have just become independent and are dispersing from their natal territories. The interpretation is that vocal behaviour at this time advertises that a territory is occupied. For instance, the peak season of vocalizations for Japanese Scops-owls is from September to December, and male Ural Owls engage in hooting exchanges in the autumn months in central Sweden. Interestingly, the frequency of hooting among resident *Bubo* species, such as the Great Horned Owl and the Cape Eagle-owl (*Bubo capensis*), increases in mid-winter in temperate latitudes and peaks just before egg-laying. This pattern is repeated in the Spectacled Owl, which breeds from January to May in Costa Rica and gives primary songs only from January through to the end of March. Because the period of parental care of juveniles is prolonged in these species, the period of juvenile dispersal may overlap the time of increased pair-bonding and advertisement for mates.

Nomadic or migratory species vocalize most often when they are advertising territories or establishing new pair-bonds just prior to breeding. For example, the migratory Oriental Scops-owl begins calling in May on its Japanese breeding grounds, in contrast to the autumn calling period of its close relative, the resident Japanese Scops-owl. Vocalizations used to attract mates or to advertise nest-sites, in other words the primary songs, are given early in the breeding season by such non-resident species, usually in late winter or spring in temperate latitudes. Among *Asio*, *Aegolius* and some *Ninox* species, these primary songs are given exclusively by males and function almost solely to attract mates and advertise nest-sites. While trying to attract a mate, a male Northern Saw-whet Owl will deliver its monotonous, tooting

Like many groups of birds, strigids perform a number of actions relating to comfort behaviour. The commonest of these is wing- and leg-stretching, perfectly demonstrated by this Short-eared Owl perched on a fence post in evening light. Since these movements are frequently carried out before a period of foraging, or during a break between two such bouts, they probably serve not only to stretch the muscles and put the feathers in order, but also to ensure that the bird's circulatory and muscular systems are properly prepared for the important activity of hunting.

[*Asio flammeus suinda*, Patagonia, Chile.
Photo: Beth Davidow/
Planet Earth]



whistle almost continually all night; once a pair-bond is established, however, the male abruptly stops singing and generally restricts its vocalizing to brief calls uttered during food deliveries.

In many other owls, both members of the pair produce similar songs for territory advertisement, courtship and pair-bonding. In almost all of these species, the female's vocalizations are higher-pitched than those of the male, because, in the majority of strigids, the female's syrinx is smaller than the male's. The calls of female Verreaux's and Blakiston's Eagle-owls are lower-pitched than those of their respective mates. The double "buu-bu" song of Blakiston's Eagle-owl seems to function primarily in mate attraction or pair-bonding; within mated pairs it is given only by the male to initiate calling duets, but it is also uttered by unpaired owls of both sexes. Males vocalize more often than females in most species that have been studied, including the Flammulated Owl, Eastern Screech-owl, Great Horned Owl, Barred Owl and Ural Owl.

Intraspecific differences in the primary songs of owls are usually great enough to permit individual identification, even among species with relatively simple songs such as the Eurasian Pygmy-owl. Females may be able to use the primary songs of males as indicators of male quality. For example, B. Appleby and S. M. Redpath found that the sound frequency, or pitch, of songs given by male Tawny Owls in Britain was inversely related to body mass, and that the vibrato section was longer in larger birds, although no vocal characteristics seemed to be related to breeding success. Interestingly, males with parasitic infections produced shorter songs of higher frequency. In Italy, P. Galeotti determined that the rate and the harshness of songs ("hoots") uttered by male Tawny Owls were positively related to aggressiveness in response to song playback, which Galeotti equated with the male's "resource holding potential". The duration and the frequency range of hoots were correlated with reproductive output and the number of years over which a territory was occupied. Because males increased their rate of hooting when females joined them in vocal displays, Galeotti suggested that male hoots functioned in female choice.

New World *Otus* generally have two distinct song types that are used in territorial and courtship contexts. The Whiskered Screech-owl gives a series of hollow, whistled notes to advertise its territory, but often switches to a staccato "Morse code" vocalization when duetting with a mate. These two types of song have been well studied in the Eastern Screech-owl, which has a trilled song and a descending whinny. G. Ritchison and associates noted that trilled songs are given by both sexes, but predominantly by males, and are used in both territorial and courtship situations. Males use a prolonged version of the trilled song to advertise a prospective nest-site, and mated pairs often duet using the trilled song. Whinny songs are used almost exclusively for territorial advertisement and defence. Two neighbouring males may begin a territorial encounter with whinny songs, but then switch to trilled songs after they have approached each other. The louder, highly modulated whinny song is well suited to long-distance territorial proclamations, because it carries better through thick forest.

Mated pairs of many owl species frequently duet, particularly at the beginning of the breeding season. Males usually initiate duets, and the female replies immediately after the male's call, or even before his call has ended. The male Pel's Fishing-owl gives a sonorous hoot followed by a deep grunt, "hooooommm-hut"; the female answers this with a higher, softer hoot followed by a shorter second double-noted "hoot-oot". The male Blakiston's Eagle-owl gives a double "buubu" call that is followed immediately by the female's lower "bu." In the Spotted Eagle-owl, the male gives a primary "hoo-whoohoo" song, which is sometimes followed so closely by the female's slightly higher-pitched song that the two vocalizations sound like only one. Similarly, female Eurasian Scops-owls often duet so closely with their male partners that the monotonously repeated calls sound like a single, but two-part, call. The calls of two or more adjacent male scops-owls, while given at a very regular rate, are not synchronized with each other, and the pattern of calling thus differs from that of duetting mates. Duetting bouts in the Eastern Screech-owl are

A vital aspect of an owl's daily maintenance routine involves bathing. This has been recorded for many species, including the Austral Pygmy-owl, and almost certainly occurs among all members of the Strigidae. Standing in shallow water, as at the edge of a pool or river, the owl ruffles up its feathers and repeatedly dips its breast and head while vigorously shaking its body, so that its entire plumage is wet or damp.

This is followed by a session of feather-oiling and preening, made easier by the preceding wetting of the plumage. Further maintenance activities include sunning and dusting.

[*Glaucidium nanum*,
Torres del Paine
National Park, Chile.
Photo: Günter Ziesler]





usually initiated by the male, and consist of trilled "bounce" songs that serve to identify the individual callers and advertise the presence of a mated pair.

Owls also emit a wide variety of calls to solicit feeding or copulation, to show alarm, to discourage predators, or simply to maintain contact with their mates or young. These calls are less familiar than primary songs, and full repertoires are known for only a few species. S. Bondrup-Nielsen provided a thorough account of the vocalizations of the Boreal Owl, identifying six adult calls and two nestling calls. The primary territorial and mate-attracting song is given exclusively by the male. He also gives a softer version of this song to advertise the nest-hole to a prospective mate and to announce his arrival with food. The female answers the male's song with a "chuuk", and responds to the feeding call with a high-pitched begging call that perhaps is homologous with the begging calls given by nestlings. A low-intensity "moo-a" is given in contact situations, and a high-intensity "skiew" alarm call is given as a warning to territorial intruders and perhaps to potential predators. A very similar array of vocalizations is given by the closely related Northern Saw-whet Owl.

Another common type of repertoire is that of Verreaux's Eagle-owl. The primary song of this species is a grunting "hook hook", given by both sexes; a fast series of hoots is also used in courtship. The male gives a soft bubbling call to advertise the nest-site, and both adults emit "whok" alarm notes. The food-begging call of adult females and young is a long, hissing whistle; younger nestlings cheep and chitter.

J. Olsen and S. Trost studied the repertoire of the Southern Boobook in Australia and noted five main vocalizations. The "boobook" vocalization was given only by males, apparently as a territorial advertisement song as well as to communicate with the female. Males also gave a "croak" call while engaged in vocal duels with neighbouring males. Females gave a single hoot in reply to the "boobook" call, as well as a "bray" call. The latter was usually used in soliciting food, and perhaps copulations, from males. Young birds uttered "trill" calls while begging for food; this call may develop into the "bray" call in females.

When Eastern Screech-owls first detect a potential predator, they give a low-intensity warning to mates and young with

standard trill and whinny calls. If the threat is perceived as more serious, they give loud bark and screech calls, presumably as a warning to the potential predator or intruder. One of the most interesting alarm calls is the rattling "hiss" produced by young Burrowing Owls when something threatens them in their burrow. This call is unnervingly similar to the sound of an alarmed prairie rattlesnake (*Crotalus viridis*), and it certainly causes human intruders to think twice before reaching into a burrow. Indeed, experimental tests of the Burrowing Owl's rattle call led M. P. Rowe and associates to conclude that the call is a form of Batesian mimicry that the owls use to discourage predators from entering nest burrows.

During the early stages of the nestling period, most owlets give high-pitched chirping calls when hungry; these begging calls gradually change to species-specific hisses or shrieks as the birds get older and leave the nest. Nestling and fledgling Flammulated Owls repeatedly utter a short gasping call when hungry, whereas young Southern White-faced Owls emit a long hissing "hooooow" lasting up to 35 seconds. Juvenile begging calls often develop with age into adult contact calls, or into solicitation calls used by females during courtship. For instance, juvenile Spotted Owls give a raspy whistle when begging for food; after six months of age, this call changes to the purer, whistled "coo-whoop" given as a contact call, primarily by adult females. The female African Wood-owl often delivers a high "wheow", which the male answers with a single low hoot or a series of hoots.

One sound that is probably common to all owls, although it is not a vocalization produced in the syrinx, is the bill-snap. This loud popping noise is made by owls from as young as a few days old, and is used when a predator or other perceived threat is very close. Another mechanical sound used by species of the genus *Asio* is the wing-clap. Both sexes wing-clap in courtship and in agonistic encounters, but the sound is produced most regularly by males during courtship flights. Male Northern Long-eared and African Long-eared Owls wing-clap singly at irregular intervals, whereas male Short-eared Owls wing-clap in a rapid series, especially during aerial courtship displays.

Food and Feeding

More is known about the food habits of owls than any other aspect of their ecology, perhaps because diet is one of the easiest facets of their biology to study. This statement might seem counterintuitive given that actual observations of foraging owls are quite scarce. Our knowledge of the food habits of owls is based mostly on analyses of their pellets, which are compact packages of hair, bone and other indigestible items that owls regurgitate after finishing a meal (see Morphological Aspects). A widely under-appreciated fact is that pellets are produced also by many species of non-raptorial birds, including cormorants (Phalacrocoracidae), herons (Ardeidae), gulls (Laridae), waders (Scolopacidae), shrikes (Laniidae), crows (Corvidae), nuthatches (Sittidae) and even wood-warblers (Parulidae). Owl pellets, however, are especially large and compact, and thus are persistent in the environment and easy for researchers to find. Moreover, because owl pellets often contain the identifiable remains of small animals, they provide a reasonably accurate and easily quantifiable sample of the types of foods eaten by owls.

Owls feed on a wide variety of vertebrates and invertebrates. While nothing at all is known about the diet of approximately two dozen species of strigids, it is probably safe to say that all owls are exclusively carnivorous. Although plant matter has been reported in the diets of several owl species, the consumption of such vegetable material has been well documented only for the Little Owl. One must wonder whether some of the plant material that has appeared in stomach contents and pellets of owls actually originated in the digestive tracts of animals eaten by the owls. Suffice it to say that virtually all strigids make their living by dispatching live animals, although several species feed on carrion from time to time.

Owls and the diurnal birds of prey, the Falconiformes, have converged on a raptorial lifestyle. Not surprisingly, the two groups resemble each other morphologically, and they overlap widely in

An additional important part of maintenance behaviour is self-preening, also known as autopreening. This generally follows application of oil from the preen gland, and its primary functions are to remove any soiling or debris from the plumage and to ensure that all the feathers are properly arranged. Here, a Great Grey Owl is preening its tail feathers in the shade of a tree trunk; the intricate and delicate patterning of the plumage is shown well in this view.

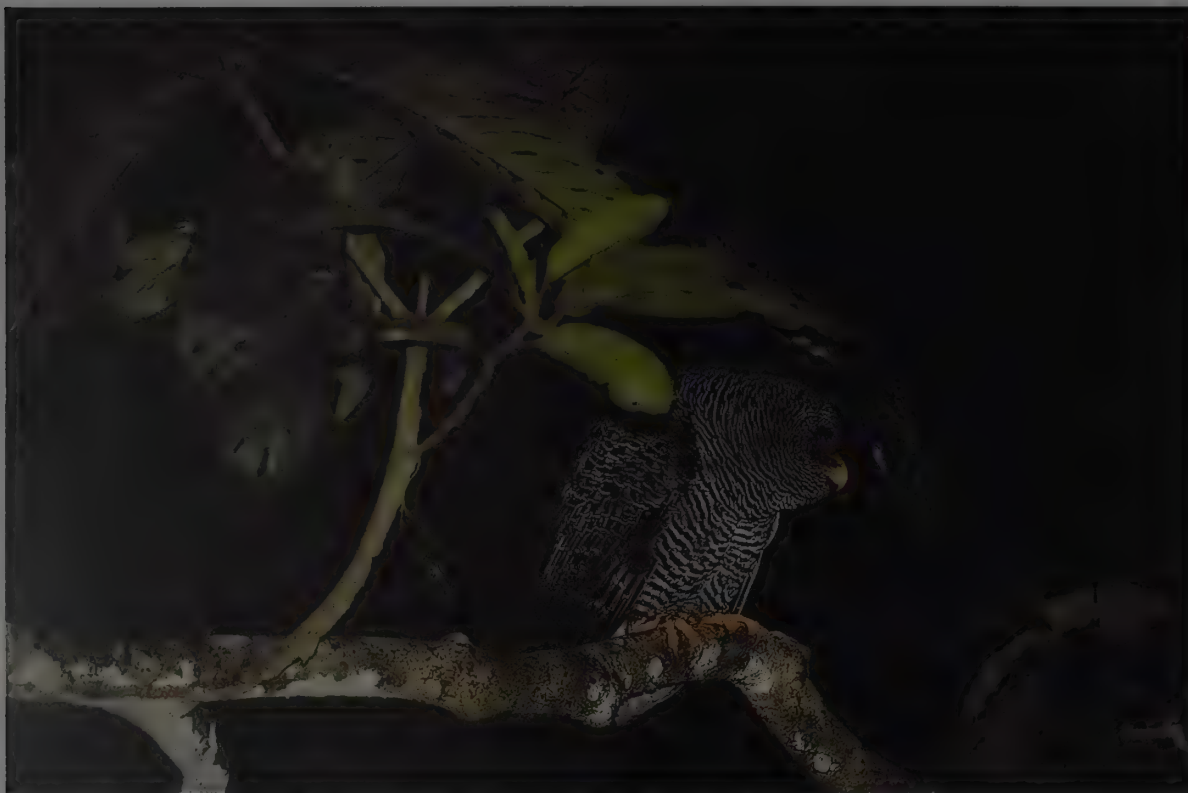
[*Strix nebulosa nebulosa*, Yellowstone National Park, Wyoming, USA. Photo: Beth Davidow/Planet Earth]

One of the 17 species of Strigidae for which allopreening has been recorded is the Burrowing Owl. This distinctive behaviour, which is widespread among avian families, involves the preening of one individual by another, and is often reciprocal. In most cases it seems to be practised by the two members of a pair, although it occasionally occurs between an adult and its young, or among siblings.

The function of allopreening is not fully understood. One proposed explanation is that it serves to reduce or redirect aggression, but this would seem not to apply in the case of owls. With strigids, allopreening appears to be a ritualized kind of behaviour, being carried out in a peaceful and non-aggressive manner. Furthermore, since the preening bird frequently performs this action on those parts of the other bird, usually the head, which are difficult for the latter itself to reach, it is likely that the behaviour also plays a role in feather care. Although allopreening has been recorded for only a comparatively small number of owl species, all of which are relatively well studied, one may speculate that it is carried out by many more species; for birds that are rather secretive and largely nocturnal, such behaviour would be difficult to observe.

[*Athene cunicularia hypugaea*,
Salton Sea,
California, USA.
Photos: Rob Curtis]





The majority of owls are night-time hunters, and a good many are strictly nocturnal, rarely seen during the daytime unless located by chance at their roost. The latter category includes nine genera, all the members of which are, with only few exceptions, active only at night. A typical example is the genus *Strix*. This Black-banded Owl was photographed at night, about 30 m above ground in lowland rainforest.

[*Strix huhula huhula*, Napo River, north-east Ecuador. Photo: Robert Behrstock]

diet. Because of their nocturnal habits, however, the owls have a somewhat limited repertoire of foraging methods compared with diurnal raptors. For example, a carrion-feeding guild, such as occurs among the Old World vultures, is absent in the Strigiformes. Unlike several species of New World kites (Accipitridae), no owls specialize on gastropods. Nor do any reptile specialists exist among the owls, in contrast to the snake-eagles (*Circaetus*), serpent-eagles (*Spilornis*) and *Leucopternis* hawks, and no owls have evolved to pursue birds in fast-flying tail-chases in the manner of many species of falcon (*Falco*).

In general, the size of an owl is correlated with the size of its prey, but the frequency distribution of prey size is skewed towards smaller species such that large owls often take small prey items. For instance, breeding Snowy Owls, which weigh 1800-2300 g, feed mostly on lemmings that weigh 50-80 g, and Eurasian Eagle-owls and Great Horned Owls, at 2500-4000 g and 1200-1700 g, respectively, routinely eat rodents weighing only 30 g and even take shrews less than 10 g in mass. In short, the larger owls probably seldom pass up a small mammal that presents itself at the right place and time, which may result in a great deal of overlap in food habits among co-existing owls of vastly different sizes.

Most owl species that inhabit the tropics incorporate invertebrates into their diet to some extent. Of the 40 species of *Otus* for which dietary information is available, 75% appear to be insect specialists. The proportion of invertebrates in the diet tends to decrease with increasing latitude, but two species of *Otus* that inhabit temperate latitudes, the Flammulated Owl and the Whiskered Screech-owl, feed almost exclusively on invertebrates. Major insect groups in the diets of *Otus* include moths, beetles and crickets. These may be caught on the ground by pouncing from a perch, or snatched from the forest canopy or out of the air after a short sallying flight. Most strigids use their talons to capture insects, but some smaller species seize moths and other flying insects in their bills, much as tyrant-flycatchers (Tyrannidae) do. An 1899 account of an Andaman Scops-owl (*Otus balli*) feeding on caterpillars stated that "it sidles up and down the boughs of small trees in a very parrot-like manner". Presumably, it used its beak to pluck caterpillars from the vegetation, but few details were provided.

Within the tropics, the proportion of insects in the diet also decreases with increasing body size of the owl. Yet, in Africa, Fraser's and the Akun Eagle-owls feed almost entirely on in-

sects. The latter species has especially small feet and weak talons for an eagle-owl, and it feeds mostly on cockroaches and beetles. Other strigids that are largely insectivorous include the Elf Owl from the deserts of the American South-west, the Maned Owl from Africa, the Crested Owl from the Neotropics, the Brown Hawk-owl from Asia, the Jungle Hawk-owl from New Guinea, and the Christmas Hawk-owl from Christmas Island in the Indian Ocean. Most of the evidence for insectivory comes from pellets, but Christmas Hawk-owls have been observed plucking moths and beetles from the foliage of the forest understorey, as well as hawking insects in the light cast by streetlamps.

Although no owl specializes on non-insect invertebrates, many non-insect prey are consumed by strigids. Eurasian Scops-owls, Tawny Owls and Little Owls are well known for their habit of pulling earthworms from the ground with the beak, and the Laughing Owl of New Zealand has also been reported to take earthworms. Crayfish and crabs are eaten by several species of *Bubo*, *Ketupa* and *Scotopelia*, and by the Brown Hawk-owl; scorpions are consumed by Western Screech-owls, Northern White-faced Owls, Great Horned Owls, Cape and Pharaoh Eagle-owls, and Hume's Owls; leeches occasionally fall prey to Eastern Screech-owls; and Whiskered Screech-owls, Great Horned Owls and Palau Owls feed on centipedes. Pel's Fishing-owl sometimes eats mussels, and Eastern Screech-owls, Spotted Eagle-owls and Barred Owls have been known to catch snails. Analysis of stomach contents of road-killed Northern Saw-whet Owls in the Queen Charlotte Islands, off western Canada, revealed that the birds had consumed intertidal invertebrates such as amphipods and isopods.

As their names suggest, the fish-owls and the fishing-owls are the closest thing to fish specialists among the strigids, although none of the six species in these two genera feeds exclusively on fish. All six species, plus Blakiston's Eagle-owl, are closely tied to fresh water, where they capture aquatic organisms at or just below the surface. Fish-eating owls typically swoop down to the water from a perch to catch fish, but Blakiston's Eagle-owl, the three fish-owls and Pel's Fishing-owl are also known to seek prey by wading in shallow water. Whether fish are detected by sight or sound is not known with certainty, but at least one species, the Tawny Fish-owl, often catches fish in broad daylight, and Blakiston's Eagle-owl will stand near holes in the ice, waiting for potential victims to come to the surface; presum-



While nocturnal hunting is the norm among the Strigidae, many species also hunt at dusk and dawn, and sometimes even during the day. One of the better-known daytime hunters is the Short-eared Owl. Although this owl will forage during the dark hours of the day, it is by no means uncommon for it to be on the wing and actively seeking prey in the late afternoon, or at times earlier, especially in the northern hemisphere.

[*Asio flammeus flammeus*,
Cambridgeshire, England.
Photo: Alan Williams/
NHPA]

ably, prey is detected by sight in both cases. Because species of *Ketupa* and *Scotopelia* lack sound-dampening fringes on their outer primaries, it might reasonably be concluded that their ability to locate prey by sound is not especially well developed. Five other species that feed to some extent on fish, namely the Eastern Screech-owl, Great Horned Owl, Eurasian and Verreaux's Eagle-owls and Barred Owl, are generalists that take a great variety of prey types and perhaps only rarely ignore a potentially suitable prey item, be it on land or in the water.

Amphibians are not a major food of any species of strigid, but frogs are fairly common in the diets of fish-owls and fishing-owls. Tree-frogs (Hylidae) are prevalent in the diet of the endangered Seychelles Scops-owl (*Otus insularis*), and various types of frogs are eaten by at least two dozen other species spread among the genera *Otus*, *Gymnoglaux*, *Bubo*, *Strix*, *Pulsatrix*, *Glaucidium*, *Athene*, *Aegolius*, *Ninox* and *Asio*; presumably, frogs have gone unnoticed in the diets of other species, too. Certainly, the numerous species of tree-frogs that are vocal at night must be eaten by many species of *Otus* in the tropics. Burrowing Owls in Minnesota, USA, were observed to catch "at least as many amphibians as mammals, yet only mammalian remains were found in pellets". In the desert of south-western Idaho, Burrowing Owls routinely stockpile spadefoot toads (*Spea intermontana*) at the entrances to their nesting burrows, only for the toads to be seemingly ignored by the hungry owlets. Both cases suggest that Burrowing Owls sometimes catch anurans and then find them unpalatable. Eastern Screech-owls and Barred Owls are among the few strigids known to eat salamanders.

Many reptiles are diurnal, and they seldom figure prominently in owl diets. Snakes are eaten, albeit in relatively minor proportions, by various species of *Otus*, *Bubo*, *Ketupa* and *Strix*. Rattlesnakes (*Crotalus*) are among the reptilian prey taken by Great Horned Owls in western North America, and a recent study revealed that snakes and lizards made up nearly 16% of the prey items taken by a nesting pair of this large strigid in the desert of Baja California, Mexico. Eurasian Eagle-owls, too, sometimes include adders (*Vipera berus*) in their diet. Barred Owls in the south-eastern USA are known to eat baby alligators (*Alligator mississippiensis*) and the occasional turtle.

The work of F. R. Gehlbach on Eastern Screech-owls of the subspecies *hasbroucki* is especially interesting with regard to rep-

tilian prey. Gehlbach found nine species of snake among the prey items cached in nestboxes and natural cavities over a twelve-year period in central Texas, USA. Interestingly, one species, the Texas blind snake (*Leptotyphlops dulcis*), was often carried alive to the owl nests, whereas all other prey was delivered dead. Although these snakes were occasionally consumed by the owls, most of them remained alive in the nest-cavity debris, where they ate insect larvae such as fly maggots. Owlets in nests with live blind snakes grew faster and had a higher rate of survival than those from nests without live snakes, perhaps because, in the absence of these reptiles, the insect larvae competed with owlets for prey delivered by the adult owls. Gehlbach suggested that the relationship was commensal, with the screech-owls benefiting from increased reproductive success and the snakes being unaffected by transport to a nest with a rich source of food. Without question, the owls did attempt to kill the snakes, as evidenced by Gehlbach's direct observations on two occasions and by talon wounds on live snakes found in the boxes. Blind snakes that survived the experience, however, remained in the boxes without further injury until two to seven days after the owlets had fledged, presumably leaving in response to the lack of food that resulted after the owls stopped attending the nests.

Species of *Glaucidium* feed on reptiles to a greater degree than do any other strigids. This makes perfect sense, given that pygmy-owls and owlets are the most diurnal of the strigids that live in warmer climates, where reptiles are abundant. Lizards are known to occur in the diets of fully 70% of the *Glaucidium* species, and the true proportion is probably higher, because no information on food is available for several species. The importance of lizards for one species of this genus was demonstrated by G. A. Proudfoot's study of Ferruginous Pygmy-owls at the northern edge of their range in South Texas. Using a combination of prey remains, video recording and direct observation, Proudfoot determined that the owls fed on 36 different prey species, with nine species of lizards making up 22.5% of the prey remains found in nest cavities. Video recordings and observations from hides revealed that the owls were largely diurnal, which corroborated anecdotal information on foraging behaviour in the heart of this owl's range in Central and South America.

Many nocturnal owls probably obtain most of their avian prey opportunistically. This likelihood is based on the fact that most

of their prey species are diurnal and thus would not be active while the owls are hunting. Examples illustrating this point include Western Screech-owls in Idaho that feed on communally roosting Common Starlings (*Sturnus vulgaris*) and Red-winged Blackbirds (*Agelaius phoeniceus*); Great Horned Owls in Canada that take American Coots (*Fulica americana*) from open-water roosts at night; Forest Eagle-owls in Asia that take Kalij Pheasants (*Lophura leucomelanos*) and Red Junglefowl (*Gallus gallus*) from their night-time roosts; and Northern Long-eared Owls in Iraq that prey on roosting House Sparrows (*Passer domesticus*). Crepuscular strigids may take a more active role in the pursuit of avian prey. Breeding Eastern Screech-owls in central Texas concentrate their hunting efforts around dawn and dusk; they often take passerines that are foraging when visibility, and thus the ability to detect predators, is reduced. The larger strigids may actively pursue smaller owls and other nocturnal species at night. H. Mikkola's thorough review of owl predation on other owls in Europe revealed 768 records of Eurasian Eagle-owls killing Northern Long-eared Owls and 286 records of their killing Tawny Owls, with Barn Owls (*Tyto alba*), Little Owls and Boreal Owls also taken in fairly high numbers. In addition, Mikkola uncovered twelve records of Ural Owls preying on Boreal Owls, and 23 cases of Tawny Owls eating Little Owls. It should be noted that, because the total number of prey items exceeded 22,000 for the Eurasian Eagle-owl and 4000 for the Ural Owl, other strigids represented only a small fraction of each species' overall diet. At least eight species of owl have been recorded in the diet of

the Great Horned Owl in North America. On Protection Island, off the coast of Washington State, breeding Great Horned Owls feed almost exclusively on Rhinoceros Auklets (*Cerorhinca monocerata*) that attend a large nesting colony at night, and nocturnal seabirds are major food items for some Short-eared Owls that inhabit the Galapagos Islands.

Perhaps the most interesting manner in which owls prey on other birds is by active pursuit during the day. Diurnal hunting is a necessity at high latitudes, where there is more or less 24-hour light during the summer months. Breeding Snowy Owls feed mostly on lemmings and voles, but also take ptarmigans (*Lagopus*), various waders (*Charadrius*, *Numenius*) and nestling passerines. Alcids, waterfowl, Eurasian Black Grouse (*Tetrao tetrix*), Grey Partridges (*Perdix perdix*) and Rock Doves (*Columba livia*) are among the avian prey of this owl in winter. Indeed, along the British Columbian coast of western Canada, wintering Snowy Owls seem to specialize on waterfowl, especially Mallards (*Anas platyrhynchos*), Northern Pintails (*Anas acuta*) and American Wigeons (*Anas americana*). With its long tail, pointed wings and powerful flight, the Northern Hawk-owl resembles an *Accipiter* hawk or a falcon, and it is also diurnal to a large extent. Although mammals dominate its diet during the breeding season, in winter it tends to take more birds, including grouse, woodpeckers (Picidae) and jays (Corvidae).

Pygmy-owls and owlets are the champion bird-pursuers among the strigids. Birds have been recorded in the diets of 83% of the 23 species of *Glaucidium* for which dietary information is



Owls, like the diurnal birds of prey (Falconiformes), are essentially carnivorous. Indeed, for those owl species for which at least some dietary information is available, they would appear to be exclusively so. A wide range of vertebrate and invertebrate prey is taken, in most cases the food being located by audial clues. The method of capture employed by strigids is characteristic. As demonstrated by this Tawny Owl on the point of seizing a mouse, the owl extends its legs and feet fully downwards and, with feet together, opens its toes to form a rectangle; then, on impact, it rapidly squeezes its talons together to kill the prey, often biting the back of the victim's skull immediately thereafter as if to make certain.

[*Strix aluco sylvatica*,
Shropshire, England.
Photo: J. Hawkins/FLPA]

Despite their renown as predators of the night, some owls can regularly be seen hunting by day, especially at high latitudes, where local conditions can require this in both summer and winter, though for rather different reasons.

The Magellanic Horned Owl of the southern half of South America is mainly active around dusk and dawn, but can sometimes be seen hunting by day. This form has recently been split from the Great Horned Owl (*Bubo virginianus*), on the basis of its much smaller size, together with its quite different vocalizations, and also its DNA.

[*Bubo magellanicus*,
Tierra del Fuego, Chile.
Photo: Günter Ziesler]



available. Data summarized by H. Mikkola show that birds make up 44% of the diet of nesting Eurasian Pygmy-owls in Finland, 37% in Sweden, 56% in Norway, and up to 80% in central Europe. Birds are also a prominent component in the diets of Collared Owlets in Asia, Andean Pygmy-owls in South America and Northern Pygmy-owls in the USA. Indeed, many individuals of the last-mentioned species vacate the mountain forest in winter to reside in suburban neighbourhoods, where they terrorize House Finches (*Carpodacus mexicanus*) and House Sparrows at bird-feeders. Some pygmy-owls routinely kill birds that are larger than themselves. For example, Ferruginous Pygmy-owls dispatch Eastern Meadowlarks (*Sturnella magna*); Austral Pygmy-owls prey on juvenile Chilean Tinamous (*Nothoprocta perdicaria*) and adult Eared Doves (*Zenaidura macroura*); and Northern Pygmy-owls have been observed killing American Robins (*Turdus migratorius*) and Pine Grosbeaks (*Pinicola enucleator*). These large prey items are almost certainly too heavy for the owls to lift in one piece. In the cases of the robin and the grosbeak, each owl pulled its victim to the shelter of an overhanging shrub, where it proceeded to pluck and consume it. Perhaps the "false eye-spots" displayed by many pygmy-owls and owlets (see Morphological Aspects) function to reduce predation on the owls themselves while they are busy processing prey items that are too large to be transported to the safety of a tree.

Fledgling birds are actively hunted by Eastern Screech-owls, Snowy Owls and Eurasian Pygmy-owls, and many other strigids probably take fledglings opportunistically. No species of strigid, however, is known to be an egg predator. Eggshell fragments found in Northern Long-eared Owl pellets during the breeding season in the USA and Norway suggest that females eat the shells of their hatched eggs, presumably for the purposes of nest sanitation rather than for the nutritional value of the shells.

Small mammals such as shrews, mice, voles, lemmings and rats are major prey items for many strigids, especially in temperate and sub-Arctic latitudes. All of the Holarctic species feed primarily on small mammals, and some Snowy, Boreal and Short-eared Owls are so dependent upon voles or lemmings, whose populations are cyclical, that individuals wander from place to place, settling to breed only in areas where such rodents are abundant. The dependence on cyclical rodents may vary with latitude. For instance, in the northern part of their range in North

America and the western Palearctic, Northern Long-eared Owls feed mostly on voles and are highly nomadic. In the deserts of the Great Basin and the south-western USA, however, they feed more on non-cyclical species such as deer-mice (*Peromyscus*) and heteromyid rodents (*Perognathus*, *Dipodomys*) and do not appear to be so nomadic. Similarly, Short-eared Owls are migratory and/or nomadic in the northern half of their range in Eurasia and North America, where cyclical voles typically account for more than 90% of their diet, but they are less nomadic or even sedentary in the southern part of their range and in the Galapagos and Hawaiian Archipelagos, where cyclical rodents are absent.

Bats are incidental prey items for many strigids, especially *Otus*, *Bubo*, *Strix* and *Ninox*, although no species, except perhaps the Black-and-white Owl, specializes on them. Some individual owls have learned to take advantage of large concentrations of bats. Each night during the summer, at sunset, a dense stream of Mexican freetail bats (*Tadarida brasiliensis*) pours out of Carlsbad Cavern in New Mexico, USA. Over the years, there are many reports of one or two Great Horned Owls flying back and forth through this virtual river of bats until they succeed in seizing a hapless one from the air; the owls cannot outmanoeuvre the bats, and so they grasp into the crowd rather than single out individuals. An Eastern Screech-owl was observed attempting to snatch little brown bats (*Myotis lucifugus*) in a similar manner as they entered a communal roost in an abandoned farmhouse in Ontario, Canada, and in South Dakota, USA, a researcher watched a small owl, probably that same species, grab a silver-haired bat (*Lasiurus noctivagans*) that had landed on a tree trunk soon after leaving a roosting cavity. In Africa, Spotted Eagle-owls have been seen catching bats that feed on insects attracted to streetlights. Similarly, in Australia, Rufous and Powerful Owls take flying-foxes (*Pteropus*) from within the forest canopy.

The eagle-owls are the world's most powerful strigids. Collectively, they take a great variety of mammals, and their diets vary widely with geography. In some parts of its range, the Eurasian Eagle-owl feeds on medium-sized mammals such as hares (*Lepus europaeus*) and rabbits (*Oryctolagus cuniculus*), but it also takes larger items such as the young of roe deer (*Capreolus*), chamois (*Rupicapra*) and ibex (*Capra*); also included in its diet are martens (*Martes*) and foxes (*Vulpes*). The Great Horned Owl, although smaller than its Eurasian relative, is nonetheless just



The prey taken by some strigids is very large when considered in relation to the size of the owl itself. This is particularly marked among the small pygmy-owls and owlets of the genus *Glaucidium*. Most members of this genus include a fair proportion of birds in their diet, catching many of their victims by actively pursuing them in flight. These owls are renowned for their ability to take prey as large as or larger than themselves, and the ferociousness of these tiny predators is borne out by the fact that they invariably elicit a fierce mobbing response from other birds that come across them. When dealing with such large prey, the pygmy-owl, unable to lift and carry off such a heavy weight, will often drag its victim to a sheltered spot, where it can consume its meal in relative safety. *Glaucidium* owls generally pluck bird prey, before swallowing the food piecemeal; since plucking can take a little time, the owl would risk being preyed on itself were it to carry out this process in an exposed position. This Northern Pygmy-owl, having successfully killed a Common Starling (*Sturnus vulgaris*), will need to act quickly.

[*Glaucidium californicum californicum*, Falkland, British Columbia, Canada. Photos: Sid Roberts/Ardea]

Invertebrates figure to a varying degree in the diet of most strigids, and a not insignificant number of owls appear to specialize on insects. Many *Otus* species fall into the latter category. The Eastern Screech-owl, for instance, takes a large number of insects, and a *Cecropia* moth affords a quite sizeable and highly nutritious meal. Since moths, beetles and crickets are mostly nocturnal, it is hardly surprising that they are widely represented among the insect prey of owls.

[*Otus asio naevius*, Pennsylvania, USA.
Photo: Joe McDonald/
Bruce Coleman]

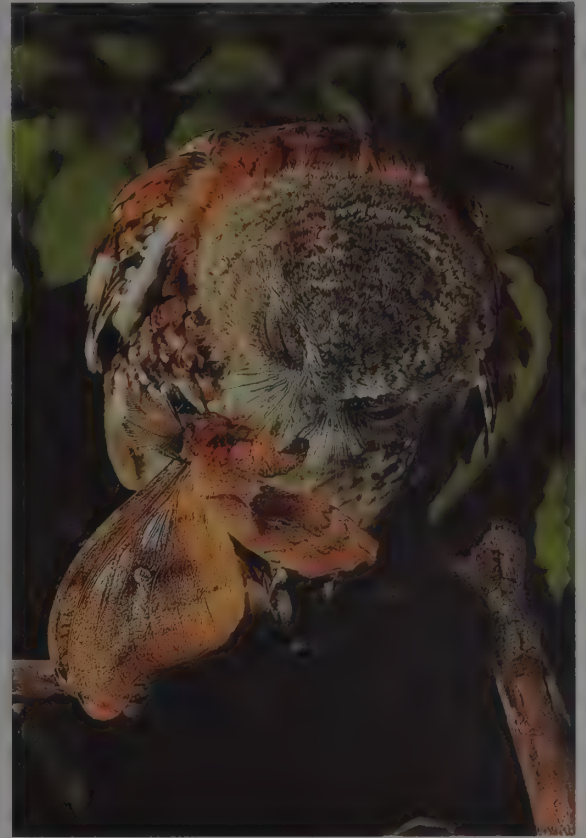
as eclectic in its choice of larger mammalian prey. Lagomorphs (*Lepus*, *Sylvilagus*) are common prey of this strigid throughout much of North America, often accounting for more than 50% of its diet, which also includes unusual prey items such as skunks (*Mephitis mephitis*), muskrats (*Ondatra zibethica*), raccoons (*Procyon lotor*) and even porcupines (*Erethizon dorsatum*). In South America, Magellanic Horned Owls take relatively small numbers of the introduced lagomorphs that occur there in abundance, concentrating instead on a variety of native mammals weighing between 30 g and 300 g. Verreaux's Eagle-owls kill hedgehogs (*Atelerix*), vervet monkeys (*Cercopithecus aethiops*), and even young warthogs (*Phacochoerus*), and Blakiston's Eagle-owls occasionally take domestic cats and dogs! The Powerful Owl is the largest and most formidable strigid in Australia, where it fills a niche similar to that of eagle-owls on other continents. Powerful Owls use their long legs and muscular feet to seize possums (*Phalanger*, *Pseudocheirus*, *Trichosurus*), sugar gliders (*Petaurus*) and other arboreal marsupials from the forest canopy, and they also snatch relatively large prey from the forest floor.

Much of the information on food habits of Neotropical owls is based on stomach contents of small numbers of collected specimens. An exception is the Guatemalan study by R. Gerhardt and associates, who monitored a single Black-and-white Owl nest for three consecutive seasons, as well as eight Mottled Owl nests. Data were gathered by a combination of pellet analysis and observations of radio-tagged males. Mottled Owls fed primarily on insects, mostly coleopterans and orthopterans, and also ate small rodents, whereas the Black-and-white Owl fed to a great extent on bats, in addition to insects. Overall, 73% of the pellets of Black-and-white Owls contained bat fur and bones, whereas only 56% of the Mottled Owl pellets contained vertebrate remains. Both species hunted from perches and were exclusively nocturnal. Mottled Owls hunted in dense climax forest, and the radio-tagged Black-and-white Owl tended to hunt in semi-open areas near ponds. The only other in-depth study of the food habits of Black-and-white Owls was in Venezuela, where, in terms of biomass, the species fed mostly on bats and small birds.

Fossil pellets dating from 10,000 years ago to late in the nineteenth century have yielded a fascinating account of the diet and ecology of Laughing Owls from the South Island of New Zealand. The owls fed on a wide variety of animals, which included at least 20 species of birds, three bats, two introduced rodents, four lizards and two frogs. Most of the prey weighed 50-150 g, and more than half of the species were nocturnal. The general picture that emerged was that Laughing Owls were opportunistic nocturnal predators that obtained most of their prey in forest habitats.

The keen ability to detect prey by sound allows some strigids to capture a prey item without seeing it. For example, Great Grey Owls and Northern Hawk-owls often capture small mammals by plunging into the snow, sometimes as deep as 45 cm, after hearing the movements of the prey. Similarly, during summer, Great Grey Owls capture pocket gophers (*Thomomys*) below ground by punching through the earthen burrows made by the gophers.

Caching behaviour is well developed in strigids, especially in species that inhabit the more northerly latitudes. Northern Hawk-owls may cache up to 20 prey items in three hours during winter, and Boreal Owls store an average of seven items in their nestboxes during peak vole years. Prey items are typically stashed in the crotch of a tree or within nesting or roosting cavities. No studies have examined how long prey remain cached before being retrieved, but some items are stored for at least several days before consumption. During summer, uneaten items would begin to rot within a few days, so long-term storage is unlikely to be beneficial. The situation is different in winter, however, when cool temperatures could preserve stored prey for weeks. The Eurasian Pygmy-owl, perhaps the most prolific food-cacher amongst Palearctic owls, tends to store rather little in summer but will put more prey items aside around the turn of the year, when the frost helps to conserve them. Indeed, cached prey animals may freeze solid during winter. Accordingly, Great Horned, Boreal and Northern Saw-whet Owls have been observed thawing frozen prey with the body, adopting a posture similar to that of an incubating or brooding female. Body heat applied to the



prey item gradually warms it to the extent that chunks of meat can be torn off and consumed.

Conventional wisdom suggests that strigids are opportunistic predators: that is, within a range of prey sizes that can be handled efficiently, most species probably take prey in proportion to its availability. In some strigids, what appears to be specialization on voles during peaks in the vole cycle can probably be attributed to voles being so abundant that they numerically dominate other available prey species. It is important to note, however, that the concept of prey availability is not restricted to the mere abundance of individuals. Perhaps in response to predation risk, some desert rodents confine their foraging to the vicinity of shrubs and other cover that will protect them from foraging owls. In addition, desert rodents such as kangaroo rats (*Dipodomys*) have inflated auditory bullae (bones in the skull) that allow them to hear flying owls, and elongated hind limbs that enable bipedal locomotion to flee from attacking owls. This anti-predator morphology may allow these species to forage in the open, and at the same time would reduce their availability to foraging owls.

Further proof that habitat selection by prey animals can influence their availability to owls comes from a study of Rufous-legged Owls carried out in the forest of southern Chile, where D. R. Martínez and F. M. Jaksic demonstrated that arboreal, scansorial (tree-climbing) and cursorial (ground-running) mammals of similar size occurred in similar abundance, yet the owls fed preferentially on the arboreal (*Irenomys*) and scansorial species (*Oryzomys*) and avoided the cursorial ones (*Akodon*). *Akodon* tended to occur in terrestrial habitats that provided overhead vegetation, whereas *Irenomys* and *Oryzomys* inhabited tree trunks and branches in old-growth forest where the Rufous-legged Owls concentrated their hunting efforts.

Most strigids use one of two basic hunting styles: "sit-and-wait" hunting from a perch, or "active-search" hunting on the wing. The great majority of species, including most *Otus*, *Bubo*, *Strix*, *Glaucidium*, *Ninox* and *Aegolius*, are sit-and-wait predators that drop or glide from elevated perches to attack prey on the ground. Strigids that use this technique, which is also known as "perch-and-pounce", tend to live in forested habitats that offer a



Small mammals are a staple food for many of the strigids. The most typical of such prey are rodents, taken by a very large number of owl species. The Southern Boobook, although mainly insectivorous, also hunts vertebrates, especially during the breeding season. This individual has captured a bush rat (*Rattus fuscipes*), a common species within the owl's Australian range. In some other parts of the world, where rodent populations are subject to cyclic fluctuations, rodent-dependent strigids are forced to adopt a nomadic way of life, breeding only where their prey happens to be abundant in any given year.

[*Ninox boobook boobook*, New South Wales, Australia.
Photo: Marco Sacchi]

large number of perches suitable for hunting. Sit-and-wait hunters also tend to have higher wing-loading than owls occupying open habitats. In contrast, some open-country strigids, especially Northern Long-eared and Short-eared Owls, have long wings and low wing-loading and use the active-search technique. Active-search foragers hunt by quartering over meadows, fields and shrubland, much as a harrier (*Circus*), and pouncing from the air on prey located by sound or sight. Flight speeds used during active-search hunting tend to be rather slow, and the owls often pull up and hover to investigate a potential prey item. Some sit-and-wait hunters, such as the Great Grey Owl, will also hover like the active-search foragers. Conversely, some of the latter, especially the Northern Long-eared Owl, occasionally hunt from a perch. Variations on the sit-and-wait technique include attacking prey within the forest canopy or in the water rather than on the ground, the first method being illustrated by some *Otus*, *Strix* and *Ninox* species and the second by the fish-owls, fishing-owls and Blakiston's Eagle-owl, while the Snowy Owl will watch from a perch but then pursue and capture its victim in flight. Northern Hawk-owls have been observed running through the snow in pursuit of small mammals, and Burrowing Owls seemingly defy classification as to hunting style, using techniques that include hovering, hopping on the ground, and aerial flycatching.

As it strikes its prey, an owl typically extends its legs and feet downwards and opens its toes, with feet together, in such a way that the eight talons form a rectangle. The eyes are closed during the actual strike, no doubt to help protect them. Prey animals are killed by a rapid squeezing of the talons, often followed by a bite to the back of the skull.

Data on capture success of owls are few, and relate mostly to diurnal species. By persistent observation, F. R. Gehlbach estimated capture success for Eastern Screech-owls and Flammulated Owls that foraged at night. The former were successful in 78% of 72 attempts; capture rate was much higher when the owls hunted insect prey, with 83% of 63 attempts succeeding, than when they pursued vertebrates, when the figure was 56% of nine attempts. When hunting insects, Flammulated Owls were successful in 81% of 31 attempts, a figure comparable to that of Eastern Screech-owls. Capture success of Great Grey Owls in the USA was 33%, and that of Ural Owls in Japan was 27%; in both cases, the birds were hunting small mammals.

Short-eared Owls observed by R. J. Clark at several North American localities were successful in only 22.5% of 577 attempts at small mammals, and Marsh Owls were reported to have a capture rate of only 20% in South Africa. Wintering Snowy Owls in Alberta, Canada, succeeded in 45% of 51 attempts when hunting from a perch; not surprisingly, their success was much higher for attempts on mammals than for those on birds, with respective figures of 54% and 15%. Similarly, wintering Snowy Owls observed in Michigan, USA, were successful in 54% of 48 attempts at mammals, but failed in all 14 of their attempts to capture birds.

One of the more thorough studies of hunting behaviour in strigids was conducted on Northern Hawk-owls in Norway by G. A. Sønnerud. Hawk-owls fly to elevated perches, from which they search intently for mammalian prey. Sønnerud erected artificial perches of three different heights in a clear-cut area of 20 ha, and observed the hunting behaviour of nine individuals over a ten-year period. Perches were placed in a uniform grid throughout the study area, but perch height varied randomly. On average, the owls visited five perches for each attack, and had to perch 13.5 times for each successful capture, which yielded an average success rate of 36%. The higher the owls perched, the farther away they attacked prey, and the farther they moved to subsequent perches. Perch height explained more of the variation in attack and move distances than did the amount of time spent at a perch, and perches from which prey was captured tended to be lower than those that were vacated without a successful capture. The data suggested that the distance between predator and prey was more important in determining whether an attempt was successful than whether a prey animal was detected, and that the movement patterns of hunting hawk-owls served to increase the efficiency with which they searched for prey.

Once an owl has caught prey, the way in which it deals with it depends on the size of the prey animal. Small items are often swallowed whole, but sometimes the head is removed and eaten and the body eviscerated; larger prey items are eaten piecemeal by tearing flesh from the body. Species of *Glaucidium* typically pluck their avian prey. The larger strigids tend to remove the wings from medium-sized or bigger bird prey, and they often discard the head and feet of large avian and mammalian victims.

Larger mammals also figure prominently on the menu of many owls. As a general rule, prey size is correlated with the size of the owl, so that the huge Eurasian Eagle-owl commonly takes hares (*Lepus*) and even bigger mammals. Interestingly, however, the frequency distribution of prey shows a marked bias towards smaller prey items. This massive predator frequently consumes small rodents weighing just 30 g, and even lighter shrews of 10 g and less. It seems that the large owls, notwithstanding their size, will take any small mammal that happens to come their way.

[*Bubo bubo hispanus*,
Madrid, Spain.

Photo: Francisco Márquez]



Most of the information on food consumption in strigids comes from captive birds, and thus represents rough estimates in the absence of active foraging and other behaviour that would normally occur in the wild. Not surprisingly, relative food consumption varies with body mass, being higher for smaller species. In the wild, food consumption also varies with ambient temperature, season of year, and activity level of the individual in question. A female Northern Saw-whet Owl weighing 96 g, and kept indoors at a temperature of 18–19°C, required 17.5 g of food per day (18% of body mass) to maintain her body mass. Two male Eastern Screech-owls that weighed 150–160 g consumed 25–33% of their body mass daily when kept in outdoor flight cages at temperatures ranging from 6°C to 21°C. C. D. Marti raised in captivity a single chick from each of three species of strigids, the Burrowing, Northern Long-eared and Great Horned Owls. Beginning when the birds were nearly one year old, Marti measured their daily food consumption in an outdoor aviary, which restricted their flight activity, over an eleven-month period at temperatures ranging from -1°C to 21°C. The Burrowing Owl, a male weighing 160–177 g, consumed an average of 15.9% of its body mass; the Northern Long-eared Owl, a female of 265–304 g, consumed 13.8% of its body mass; and the Great Horned Owl, a male that weighed 1265–1410 g, ate 4.7% of its body mass per day. Other studies of captive Great Horned Owls have estimated daily food consumption at 1.5% to 2.5% of body mass. Free-flying Tawny Fish-owls weighing 2100–2600 g were estimated to consume less than 12% of their body mass per day in Taiwan.

In an elegantly comprehensive study conducted both in the field and in the laboratory in the Netherlands, H. Wijnandts estimated gross energy intake of wild Northern Long-eared Owls throughout their annual cycle, taking into account such factors as seasonal variation in digestibility and the energetic costs of breeding, foraging, flying and moulting. On the basis of a caloric content of 8.0 kJ per gram of prey, Wijnandts calculated a gross energy intake of 292–415 kJ per day during the non-breeding season. From analyses of pellets collected throughout the year, he estimated that voles contributed 55–82% of the owls' energy intake, followed by other small rodents (3–19%), birds (4–26%) and non-rodent mammals (3–9%). Moulting was estimated to add as much as 26 kJ to the daily energy budget, and flying,

based on an average of 158 minutes of flight per night, cost 104 kJ per day.

Breeding

The mating systems of birds are difficult to study, but those of the largely nocturnal owls have proved particularly challenging. Although some classic studies have been carried out, such as H. N. Southern's work on Tawny Owls at Wytham Wood, near Oxford, England, the last two decades have seen a myriad of investigations on owl breeding biology using nestboxes, radio-telemetry, and electronic sensors at the nest, as well as more traditional observational techniques.

Bats are taken by a number of owl species, although they tend to constitute incidental additions to the diet rather than regular prey items. One reason for this may be that owls are generally designed more for silence and stealth than for rapid, agile aerial pursuit. Members of the genus *Ninox*, aptly known as hawk-owls, are amongst the more nimble fliers, and several of them are known to catch bats. This Brown Hawk-owl has caught a leaf-nosed bat (*Hipposideros*).

[*Ninox scutulata lugubris*,
Keoladeo Ghana
National Park,
Bharatpur, India.
Photo: Gertrud &
Helmut Denzau]





Most strigids are monogamous, and many species have long-lasting pair-bonds. In Finland, P. Saurola found Ural Owls to be very faithful from year to year, with an annual divorce rate of only 2.7%; Tawny Owls were less true to their mates and had a 12.1% divorce rate. Long-term pair-bonds are common in other members of the genus *Strix*, as well as in *Bubo* and *Otus*. Species of *Asio* and *Aegolius* typically form shorter pair-bonds, usually for only one season. These species tend to be rather nomadic, adult females in particular being prone to disperse

long distances from their former nesting territories during periods of low prey abundance.

Many bird species with monogamous mating systems have been found to engage in extra-pair copulations, but this seems to be rare among owls, at least in the species that have been well studied. In fact, extra-pair copulations have been demonstrated for only two species, the Burrowing Owl and the Flammulated Owl. B. Johnson found evidence of extra-pair fertilizations in two of 31 Burrowing Owl nestlings in a "loose colony" in California. In Colorado, R. T. Reynolds and B. D. Linkhart observed a female Flammulated Owl that copulated with its territorial male and an intruding male on the same night; whether the intruder fathered any of the female's young was unknown. Also in the USA, J. S. Marks and associates, using DNA fingerprinting, detected no extra-pair fertilizations in 49 Northern Long-eared Owl nestlings from ten "semi-colonial" nests in Montana in which nearest-neighbour distances averaged less than 100 m, and S. G. Lawless and colleagues obtained similar results in a genetic analysis of 80 nestlings from 23 broods of the highly territorial Eastern Screech-owl in Kentucky. In another detailed study, C. Rohner found that movement patterns of unpaired "floater" Great Horned Owls in Yukon Territory, Canada, did not change during the fertile period of females, though they would be predicted to do so if male floaters were seeking copulations with paired females. Extra-pair copulations are equally unknown in the well-studied Spotted Owl.

Eight species of Strigidae are known to be polygamous. In other bird families, polygamy is commonest in situations where the adults, especially adult males, take little or no part in the feeding of the young. In owls, however, the males are the primary providers of food for the female and the young, so polygamy is restricted to times of prey abundance. Polygamy occurs most often in species that specialize on microtine rodents as prey, because voles exhibit dramatic population explosions every three to four years. In those years, some males find it relatively easy to provision the female and young at more than one nest, so such a male will try to attract a second female to his territory once his first (primary) female is incubating a full clutch of eggs.

Polygamy has been documented in the Eurasian Scops-owl, Snowy, Tawny and Ural Owls, Northern Hawk-owl and Northern Long-eared Owl, but it is probably commonest in the Boreal

While the diurnal lifestyle of many reptiles means that they frequently avoid the predations of owls, lizards and snakes nevertheless do form a small proportion of the diet of a fair number of strigids, most notably those of the genera Otus, Bubo, Strix and Glaucidium. In South-east Asia, geckos are particularly abundant and are often active at night, so it is hardly surprising that a Sunda Scops-owl should take advantage of such a relatively easy meal. Here, the unfortunate victim is of the species Gehyra dubia.

[*Otus lempiji cnephaeus*, Singapore.
Photo: Morten Strange]



Larger reptiles, including snakes, also fall victim to owls on occasion. Although the Buffy Fish-owl feeds mostly on fish, its diet includes a wide variety of other animals, ranging from frogs, small mammals and birds to reptiles and insects. As this photograph shows, it is not averse to killing and eating snakes, but it is doubtful whether such prey ever form a significant part of this species' diet. It would be interesting to determine just how many snakes are taken by strigids living in desert habitats, where these reptiles are largely nocturnal.

[*Ketupa ketupu ketupu*, Kuala Selangor Nature Park, Malaysia.
Photo: Arnoud B. van den Berg]

Among the most specialized of the Strigidae are the fishing-owls of the African genus *Scotopelia*. The largest of these, Pel's Fishing-owl, is also the best studied of the three species.

It is known to take some amphibians and freshwater crustaceans, as well as larger insects, but by far the majority of its food consists of fish in the size range 100-200 g, though with some weighing up to 2000 g.

This very big owl frequents the forested edges of rivers and lakes, where it hunts, mainly at night, from a perch 1-2 m above shallow water.

It probably detects fish from the surface ripples they create, following which it glides down to snatch the prey from the surface. Catfish are very commonly captured in this way. Like their Asian counterparts, the fish-owls of the genus *Ketupa*, the *Scotopelia* owls have unfeathered tarsi and toes, and the soles of their feet are equipped with spiny scales, adaptations that enable them more easily to grasp their slippery piscine prey. Being largely dependent on fish, Pel's Fishing-owl breeds when water levels are low, conditions which facilitate the capture of these aquatic prey.

Of course, fluctuations in water levels occur periodically, and in periods of drought or, conversely, flooding the owl is often forced to move to nearby areas where conditions are better for it.

[*Scotopelia peli*,
Lake Malawi, Malawi.
Photo: Elizabeth Bomford/
Ardea]





In most cases, strigids use their talons to capture prey. Insects, such as orthopterans, are often taken on the ground, the owl grasping them with one foot. The bird generally then uses the same foot to transfer the food directly to the bill for consumption. This method of food transference is very reminiscent of the way in which parrots (*Psittaciformes*) deal with their food. Here, a Burrowing Owl shows how it tackles a grasshopper.

[*Athene cunicularia hypugaea*, Grasslands National Park, Saskatchewan, Canada. Photos: Stephen J. Krasemann/DRK]

and Northern Saw-whet Owls. In these species, the usual form of polygamy is bigyny, where one male is paired with two females simultaneously. This has been particularly well studied for the Boreal Owl, in which 9-14% of breeding males are bigynous in years of peak vole numbers. A bigamous male attracts a primary female to a nest cavity and feeds her at a high rate during the egg-laying and copulation periods. After the clutch is complete, the male reduces the rate at which he feeds the primary female and begins singing again, usually near a suitable nest-site some distance from the primary nest cavity. If he succeeds in attracting a second female to this new nest-site, he feeds her at a high rate until she, too, completes a clutch. Despite the difficulty in feeding extra young, bigamous males raise more offspring than monogamous males. After provisioning their secondary females with food during egg-laying, the males turn their attention back to the primary brood, and feed the secondary female and her young only if the first brood is well fed. Primary females lay more eggs than the average monogamous female, and raise as many or more young. Secondary females, however, raise relatively few young on average because of higher nestling mortality while the male is attending to the primary brood. Because their nests are some distance from the primary nest, it is generally assumed that secondary females are deceived by the male and do not know that he is already paired when they choose him as a mate. This could hardly have applied, however, in the case of one particular male Northern Saw-whet Owl, which was found to be attending primary and secondary nests only 15 m apart.

At least two instances of trigyny have been documented in strigids. J. S. Marks and associates found a male Northern Saw-whet Owl in Idaho, USA, that was paired with three females simultaneously: two of the nests fledged young successfully, but the eggs failed to hatch at the third nest. During a food-addition experiment, B. G. Carlsson and B. Hörnfeldt noted an instance of trigyny in the Boreal Owl in Sweden, although it must be added that this might not have happened under more natural conditions. It should also be noted that all records of polygamy in cavity-nesting owls have occurred where researchers provided an abundance of nest-sites in the form of nestboxes.

A rarer form of polygamy in strigids is serial polyandry, in which a breeding female leaves her first nest-site and moves to a new territory to mate with a second male. The female deserts the nest late in the nestling period, when the young no longer require brooding, leaving the first male to continue to feed them alone. In normal situations, the female usually helps to provision the young in the later stages of the nestling period. Serial polyandry has been documented only in the Boreal Owl, but it probably occurs in the Northern Saw-whet Owl and perhaps in a few other species as well. Two interesting examples of mixed biandry and bigyny have been recorded in Boreal Owls. B. Kondratzki and R. Altmüller studied a bigynous male in Germany whose primary female left the nest to produce a second brood with a different male, and E. Korpimäki noted a female Boreal Owl in Finland whose second brood was the result of her being a secondary female to a bigynous male.

Most owls breed only once per season, presumably because the length of the breeding cycle and extended post-fledging care simply rule out any possibility of a second brood. However, double-brooding has been observed five times in Florida Burrowing Owls and once in the Northern Long-eared Owl. In the latter case, the event occurred during a year of high vole abundance. Whether this was another case of serial polyandry, as described above for Boreal Owls, or a rare instance of double-brooding by the same pair was not determined.

The timing of breeding among members of the Strigidae is keyed to prey availability and vulnerability. Mammal-eating species in temperate latitudes tend to nest in late winter or early spring; this is probably in order to take advantage of the long nights, so that more time can be spent hunting for food when the young are growing. Eurasian Eagle-owls usually lay eggs in February or March throughout most of their range from Finland to Morocco, probably using the lengthening days as a stimulus to initiate nesting. Populations of close relatives in tropical zones only slightly farther south seem to exhibit less seasonality in their breeding, although data are sparse. Insectivorous species nest later at temperate latitudes, so that food is abundant during the nestling stage. Eurasian Pygmy-owls seem to time their breeding so that the nes-

ling period coincides with the fledging times of many passerine species, which are important prey (see Food and Feeding).

Those owls that nest in tropical regions with marked wet and dry seasons breed in the dry season or toward the end of it, so that the young fledge early in the wet season. This is particularly important for insectivorous species, which many tropical owls are, because it enables them to take advantage of the increase in insect numbers that occurs during the wet season. Off the coast of Tanzania, the Pemba Scops-owl (*Otus pembaensis*) lays eggs from August to October, before the short rains begin. In South Africa and Madagascar, Marsh Owls breed in March and April, after the rains have produced a lush growth of grass that in turn provides cover for nesting and forage for their rodent prey species. Pel's Fishing-owls lay at the time of peak river flow, so that their young fledge when water levels have dropped and fish are concentrated.

Many owls are particularly reliant on small mammals whose populations are subject to dramatic cycles of abundance. These cycles are very noticeable in voles, lemmings and snowshoe hares (*Lepus americanus*). The most widespread and well-studied of these situations concern owls that feed primarily on voles, including the Northern Hawk-owl, Boreal Owl, Northern Long-eared Owl and Short-eared Owl. In these species, the proportion of adults breeding, the number of eggs laid, and brood sizes at fledging vary dramatically from year to year, depending on vole numbers. Because clutch size is dependent on the condition of the female during egg-laying, females are likely to lay large clutches if they are well fed because of high prey numbers.

A. Lundberg found that breeding frequency, clutch size, and production of young in Swedish Ural Owls varied with vole abundance. H. Pietiäinen and associates reported that only 24% of female Ural Owls bred during vole lows in Finland, but 76% bred during vole population peaks; moreover, the owls laid larger eggs and initiated egg-laying earlier during peak vole years. An interesting aspect of the breeding strategies used by Boreal Owls during different parts of the vole population cycle has been studied in Finland by H. Hakkarainen and E. Korpimäki. They found that older males that had probably experienced one full vole cycle reduced their rates of food-provisioning at the nest in the peak year of the cycle compared with their rates during the phase of increase, despite the fact that prey was more abundant during the peak; the males did this by reducing feeding rates in the second half of the

night. On the other hand, the provisioning rates of young, inexperienced males were highest during the peak year of the vole population cycle. Hakkarainen and Korpimäki propose that experienced males can predict that the survival of their young would be low after a vole peak, when prey numbers crash, whereas juvenile survival during the increase phase would be very high.

Similarly, B. M. Appleby and colleagues found that Tawny Owls appear to be able to predict summer vole abundance on their territories. Clutches laid in March on territories that would have a high number of voles in June produced a preponderance of female offspring. Female Tawny Owls, but not males, appear to gain future reproductive advantages from being raised under conditions of good food supply.

Some strigid species will not breed in areas without high vole numbers. Northern Hawk-owls are especially noted for this, appearing in an area, nesting for one to three seasons, and then disappearing. C. Rohner and co-workers point out, however, that Northern Hawk-owls breeding in North America are also highly dependent on juvenile snowshoe hares for food, so their breeding success is not simply tied to vole numbers. Another well-studied predator-prey system is that of Great Horned Owls and snowshoe hares. In northern Canada and Alaska, snowshoe hares have a dramatic ten-year cycle in which they are extremely abundant for two years, after which numbers crash to near zero; they then recover about seven years later, and quickly rebuild to reach a peak again. Rohner has found that all territorial Great Horned Owls breed during the peak years, breeding numbers are reduced in the year of the hare decline, and no breeding occurs in the second and third years after the decline. During peak hare years, survival of young owls is high, and many non-breeding "floaters" are present. In the year of the decline, most juvenile mortality occurs before the young disperse from their natal territories; these birds generally die of disease and predation rather than from starvation.

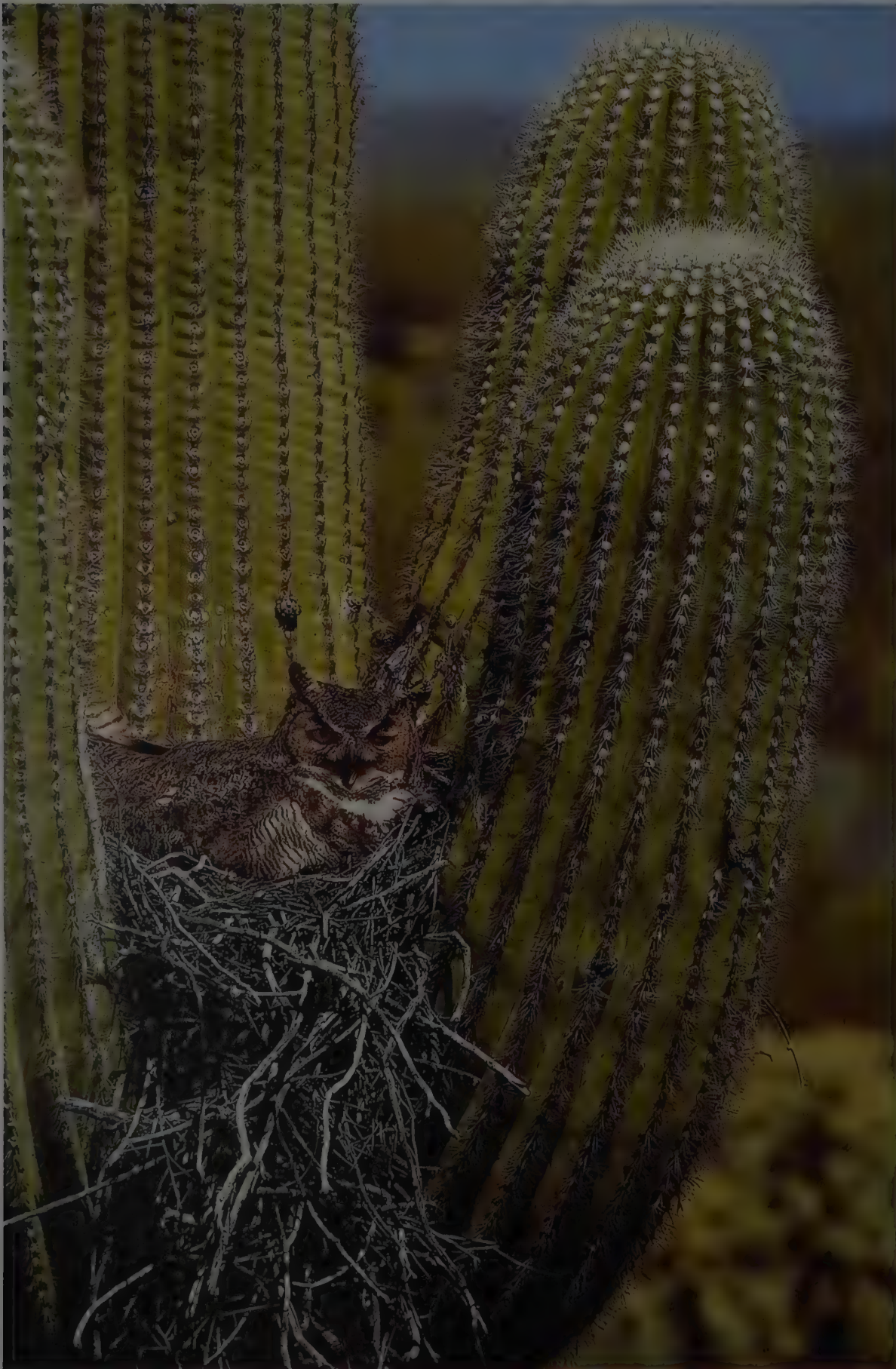
To attract a mate or to renew the pair-bond with his partner, a male owl generally begins vocalizing about a month before nesting begins. Males in the genus *Asio*, such as the Northern Long-eared, Short-eared and Marsh Owls, perform wing-clapping displays, slapping their wings together beneath the body as they fly. Marsh Owl pairs fly together in wide circles over their territory during courtship, and males of the closely related Short-eared

Although pellets are produced by a wide variety of non-raptorial birds, those ejected by owls are especially large and compact.

These packages of indigestible matter, such as bones and hair, are ejected at the daytime roost or the nest, and are often present in quantity at regularly used sites. They provide the principal source of information on the diet of owls, enabling prey species to be identified from skeletal remains. This Spectacled Owl was perched quietly at its day roost in forest; it then bent forwards to eject a pellet from the previous night's hunting. Owls normally produce one pellet per meal.

[*Pulsatrix perspicillata saturata*,
Corcovado National Park,
Costa Rica.
Photo: Kevin Schafer]





Owls do not construct a nest of their own. Instead, the vast majority breed in natural or artificial cavities, or in old nests of other birds, while some species regularly nest on the ground. Open nests are commonly used by *Bubo* owls, as well as by some species of *Strix* and *Asio*. These are usually old structures built by corvids or raptors, and typically consist of sticks and twigs. They are normally sited in a tree, but may also be on a cliff ledge or, as in the case of this Great Horned Owl, in a saguaro cactus. In most instances, old stick nests of other species are used by the owl pair for one year only, unlike hole nests, which are frequently reused in subsequent years. All breeding studies carried out on strigids reveal a strict division of labour in the roles of the sexes. The female performs all of the incubation and brooding duties, and she develops a single large brood patch for this purpose; the male provisions his mate at the nest during these periods, at least until the young are old enough to be left alone in the nest.

[*Bubo virginianus*
pallascens,
Sonoran desert,
Arizona, USA.
Photo: John Canalsoli/
Bruce Coleman]

Owl perform dramatic courtship displays high in the air. Nest displays are important in many species. Male Boreal and Northern Saw-whet Owls call from prospective nest-sites while trying to attract mates. In many ground-nesting species, typified by the Akun and Spotted Eagle-owls, pair-bonding displays include ritualized scraping at the nest-site.

In essentially every owl species, courtship characteristically involves ritualized feeding in which the male brings prey items to the female, and she in turn usually makes begging calls and movements characteristic of young owls. The presentation of food to the female is often accompanied by wing- and body-movement displays by the male, before copulation takes place. Male Snowy Owls give a dramatic "Angel-display" with outspread wings when presenting food to the female, whereas male Northern Long-eared Owls raise and lower their folded wings and "buck" the body up and down. Allopreening seems to play an important role in cementing the pair-bond, as well as being a conspicuous part of the pre- and post-copulatory behaviour of many species, including the Eurasian Scops-owl, Eastern Screech-owl and Spotted, Little and Burrowing Owls (see General Habits). Copulations are usually reported to take place shortly after dark, but it is impossible to say whether this is a true reflection of owl biology or an artifact of the behaviour of human observers, who tend to be more observant early in the evening!

Few other bird groups, the caprimulgiforms being one possible case, show such an antipathy toward nest-building as do the strigids. This is especially remarkable considering the wide variety of nest-sites used by owls. Some medium-sized and large species, such as Great Horned, Great Grey and Northern Long-eared Owls, prefer to use large stick nests built by other birds, especially corvids and hawks, but they will nest in almost any suitable situation, including cliff ledges and the tops of hollowed-out snags. In southern Africa, Spotted Eagle-owls often nest on the ground, but they also use nests built by Hamerkops (*Scopus umbretta*), hawks, eagles, corvids and Social Weavers (*Philetairus socius*). Verreaux's Eagle-owls, too, use Hamerkop nests, as well as those of storks (Ciconiidae), ibises (Threskiornithidae) and

buffalo-weavers (*Bubalornis*). White-faced owls have commonly been considered members of the genus *Otus* (see Systematics), but their habit of using stick nests built by other birds, rather than nesting in tree cavities (as do *Otus*), was one of the clues that resulted in their placement in *Prilopsis*. Southern White-faced Owls will use the larger stick nests mentioned above, but they also use smaller nests such as those built by pigeons (*Columba*), turacos (*Tauraco*), sparrows (*Passer*), waxbills (Estrildidae) and Wattled Starlings (*Creatophora cinerea*). Large squirrel dreys are used as nest-sites by many owl species around the world.

The very large Eurasian Eagle-owl usually nests on cliff ledges, but will use corvid and hawk nests if cliff sites are unavailable, and in northern Europe it will also nest on the ground next to trees. One female in Finland dug out cavities in large anthills, one of the few examples of actual nest construction in the Strigidae. Most Eurasian Eagle-owls simply remove sticks and loose stones to form a clean nest scrape.

Some owls, particularly those found in open country such as tundra and grassland, prefer to nest directly on the ground. The Striped, Short-eared and Marsh Owls nest in areas of tall grass, trampling down the stalks to form a nest platform of sorts. Owls that breed in shrubby habitats also nest on the ground, and these include the Laughing Owl of New Zealand and the White-browed Hawk-owl of Madagascar.

Smaller species of owls, such as those in the genera *Otus*, *Glaucidium* and *Aegolius*, generally nest in tree cavities that have been excavated by woodpeckers, a requirement that often makes the availability of nest-sites a limiting factor to these species (see Status and Conservation). G. D. Hayward has found that Boreal Owls in Idaho usually nest in cavities built by the Pileated Woodpecker, which often means that they must breed at lower elevations where the woodpecker is common, some distance from the owls' preferred foraging habitats at higher elevations; in Europe and Asia, this owl shows a similar reliance on the holes created by a related woodpecker species, the Black Woodpecker (*Dryocopus martius*). Some scops-owls are more adaptive, nesting in a wide variety of cavities: one African Scops-owl used a

Natural cavities in trees are among the most frequent nest-sites used by strigids, and are very typical for the smaller species. Such sites are regularly adopted by a large number of species of *Otus*, and also by many *Strix*, *Glaucidium* and *Athene* owls. The hollow interior of a broken-off limb offers a relatively secure and warm environment in which a Spotted Owlet can rear its young.

[*Athene brama indica*,
Ranthambore
National Park, India.
Photo Günter Ziesler]





recess in the side of the large stick nest of a Lappet-faced Vulture (*Torgos tracheliotus*). Larger owls in the genera *Strix*, *Ninox* and *Pulsatrix* nest in cavities that form in old trees where large branches have broken off, or where the trunk itself has broken, and Spotted Owls also utilize large clumps of tree branches formed in conifers by the action of dwarf mistletoe (*Arceuthobium*). Some

small strigids, such as the Western Screech-owl and Pallid Scops-owl, will use Black-billed Magpie (*Pica pica*) nests if tree cavities are not available. Cavity-nesting owls bring no other material to form the nest, although female Eurasian Pygmy-owls apparently clean out the nest-hole.

The Burrowing Owl is unique within the family in using underground burrows for nest-sites. Most of these are dug by fossorial mammals such as prairie-dogs (*Cynomys*), viscachas (*Lagostomus*) or badgers (*Taxidea*). The owls clean and enlarge some of the burrows, and there is some evidence that they can dig their own burrows if the soil is very sandy, especially in Florida and on islands in the West Indies.

Because owls do not build their own nests, they often accept man-made nests of varying types. Most, if not all, cavity-nesting owls will use artificial boxes. Indeed, in Finnish forests, where the large trees favoured by Black Woodpeckers are rare, about 95% of Boreal Owl pairs nest in such boxes. Eurasian Eagle-owls readily nest in lean-tos built by foresters, or in similar structures built specifically for their use, and one pair used a hide built by a nature photographer to view displaying Western Capercaillies (*Tetrao urogallus*)! A Spotted Eagle-owl once nested on a geranium box set outside the bedroom window of a house, and Great Grey Owls will nest on wooden platforms placed in trees in suitable habitats.

Nest sanitation varies from species to species. Members of the genus *Otus* tend to maintain very clean nest cavities and use the same hole year after year, whereas the cavity nests of many other species become fouled with faecal material and prey remains. Most owls that take over stick nests tend to use them for one year only, and the same applies to cavity-nesters in the genus *Aegolius*. Some researchers speculate that Boreal Owls change nest-sites every year because it lowers the risk of predation, but such changes could equally result from the cavities becoming filled with excrement and prey remains towards the end of the nesting period, rendering a new cavity more suitable than an old one. Some nestboxes have been used two years in a row by Northern Saw-whet Owls, but the boxes have been cleaned in the winter by humans, and the occupants in the second year were never the same pair as in the first year.

Owl eggs are pure white, and are usually round to oval in shape. Selection for spotted or otherwise camouflaged eggs is

A common practice among the smaller strigids is that of taking over old cavity nests of other species, especially woodpeckers (*Picidae*) and barbets (*Capitonidae*). A disused woodpecker hole in a sabal palm provides an ideal nesting site for a Cuban Pygmy-owl. In some parts of the world, particularly in the boreal region, certain species of owl appear to be heavily dependent on the existence of old woodpecker holes for breeding, to the point that the availability of such cavities is a limiting factor in their distribution and abundance.

[*Glaucidium siju siju*,
Ciénaga de Zapata, Cuba.
Photo: Doug Wechsler/
VIREO]



When it comes to exploiting the nest sites of other avian species, it is not only tree cavities that are used by strigids. Indeed, a rather wide variety of structures is made use of. In the Neotropics, for example, the oven-shaped mud nests of horneros (*Furnariidae*) are quite frequently used by several species of pygmy-owl. Here, a Ferruginous Pygmy-owl has made its home in the nest of a Rufous Hornero (*Furnarius rufus*), a common bird of open country, parks and even urban areas.

[*Glaucidium brasilianum brasilianum*,
Pantanal of Mato Grosso,
Brazil.
Photo: Edson Endrigo]

Although perhaps a somewhat incongruous sight, it is not that unusual for a Verreaux's Eagle-owl to use the colonial nests of weavers (*Bubalornis*, *Philetaurus*) as a platform for its own nest.

This adaptable and opportunistic owl will also nest at times on the top of the huge nest of a Hamerkop (*Scopus umbretta*), as well as in stick nests of storks (*Ciconiidae*), ibises (*Threskiornithidae*) and other large birds.

The distinctive pink eyelids of this owl are well visible in this photograph.

[*Bubo lacteus*,
Kruger National Park,
South Africa.
Photo: Ron O'Connor/
BBC Natural History Unit]



probably precluded by the facts that owls normally begin incubation shortly after the first egg is laid, and incubate their eggs continuously during the day. Conversely, white eggs laid in open nests may have promoted the early onset of incubation characteristic of most owl species. Round eggs are typical of cavity-nesting species, such as many strigids, because there is little danger that the eggs will roll out of the nest.

Egg size in strigids ranges from about 28 x 35 mm in the Elf Owl to 50 x 60 mm in the Eurasian Eagle-owl. Small insectivorous species, such as the Elf Owl and most scops-owls, tend to have small clutch sizes, normally 2-4 eggs, as do large carnivorous or piscivorous species in the genera *Bubo*, *Kenya* and *Scotopelia*. Species reliant on mice, voles and other small rodents generally lay larger clutches, 4-7 eggs on average, and they may lay clutches of up to nine eggs or more during periods of especially high prey abundance.

The eggs are usually laid at intervals of about two days, and incubation begins with the first or second egg. This, of course, results in nestlings of very different ages, particularly in the case of large clutches. For example, the oldest nestling in a brood of seven young would be about two weeks older than the youngest one. Asynchronous hatching has often been considered to be a brood-reduction strategy, so that, if food becomes scarce towards the end of the nestling period, the oldest, largest chicks will remain well fed, whereas the youngest and smallest often starve. Some cavity-nesting owls, however, such as pygmy-owls and the underground-nesting Burrowing Owl, tend to delay the start of incubation until most of the eggs have been laid. This suggests that the onset of incubation in owls is influenced more by vulnerability to predation than by the possibility of food limitation and subsequent brood reduction. This vulnerability to egg loss may be accentuated by the white, unmarked eggs of owls that nest in the open.

A strict division of labour occurs in all owls that have been well studied, with the female performing all of the incubation and brood-rearing duties, and the male doing all of the hunting, at least while the female is attending the nest. Incubation periods range from 22 days in small species, such as the African Scops-owl, to 32 days in larger species, such as Verreaux's Eagle-owl. Female strigids develop a single large incubation patch in the centre of the abdomen, and in most species the female remains

on the nest from several days before egg-laying begins until the time when the young are old enough to maintain body heat on their own. Females generally leave the nest only once or twice each night to defecate and cast pellets, and they do not begin to hunt for themselves until later in the brood-rearing period; indeed, in species such as the Northern Saw-whet Owl, the female is so heavy during egg-laying, reaching 150% of her normal mass, that she can fly only very laboriously. In the Boreal Owl, the female helps the male feed the young after she stops brooding, but the male continues to be the primary food-provider for the young. Female Southern Boobooks will help provision the young for two or three weeks after fledging, but the male then continues to feed them alone until they become independent about six or seven weeks after they have fledged.

As mentioned earlier, males do all of the hunting and provide all of the food for the female and young, at least for the first two or three weeks of the nestling period. The male usually calls when arriving with food, often with a subdued or shortened version of the advertising song. The transfer of food from the male to the female usually takes place at the nest, but in some species, particularly pygmy-owls, the male calls and the female leaves the cavity, takes the food, and then returns to the nest to feed the young herself. While the young are small, the male delivers the prey item to the female, and she tears it into smaller pieces for the nestlings. As the young become older and are able to feed themselves, the male may simply drop prey items at the nest without transferring them to the female. In Northern Saw-whet Owls, when the young are old enough not to require brooding, the older owlets may feed bits of prey to their smaller siblings.

In smaller mouse-eating strigids, such as *Glaucidium* and *Aegolius* species, the male often eats the head of the prey for his meal and gives the body to the female. Males of the much larger Great Grey Owl often eat whole mice themselves and carry bigger prey, such as pocket gophers, to the nest for the female and young, thus reducing the number of trips to the nest and associated flight costs.

In many species, for example the Eurasian Scops-owl, Pel's Fishing-owl, Great Grey Owl, African Wood-owl, Northern Long-eared Owl and Short-eared Owl, most of the defence of the nest is undertaken by the female, perhaps because she is usually alone at the nest-site, and because she is the larger sex. If the



Some species of owl nest on the ground as an alternative to using an elevated site, but certain species, mainly those inhabiting open country, are habitual ground-nesters. The latter are typified by the genus *Asio*, the best-known member of which is the widespread Short-eared Owl.

This medium-sized owl breeds in grassland, moorland, tundra and other open habitats, and invariably nests on the ground, in this instance among tall heather (*Calluna vulgaris*) on open moorland. The owl tramples down the vegetation stalks to form a platform, usually lining this with some grasses and downy feathers; of great interest is the fact that this species, at least in Europe, seems to make some effort to build a nest, behaviour almost unique among the *Strigidae*.

The eggs of all owl species are white and unmarked, and generally rounded to oval in shape; they are normally laid at intervals of two days, with incubation beginning with the first or second egg. A fascinating aspect of clutch size is that, among rodent-eating owls living in areas where their prey are subject to cyclic fluctuations, the number of eggs laid varies annually in accordance with prey abundance. Short-eared Owls in northern regions lay about 4-5 eggs in years with low populations of voles, but up to 10 eggs in peak vole years. In years when cyclic rodents are at extremely low levels, some owls may not attempt to breed at all.

[*Asio flammeus flammeus*,
North Uist,
Outer Hebrides, Scotland.
Photo: Peter Smith/Aquila]

male is present, he may join in nest defence or simply hoot from his roost nearby. Female Southern White-faced Owls threaten nest intruders with their talons and by snarling; the male then joins in the defence with diving attacks. In other species, for example the African Scops-owl and the Boreal Owl, the male often roosts several hundred metres from the nest and is usually unaware of any danger to it in the daytime; at night, however, male Boreal Owls actively defend nestlings from predators. In contrast, male Snowy Owls apparently defend the nest vigorously when the young are small, diving on intruders and driving them away; when the young are larger and the female can leave without fear of their becoming chilled, she takes over most of the nest-defence duties, dramatically feigning injury to lead the predator away from the nest. Male Eastern Screech-owls defend nestlings more vigorously than do females; as in the case with Snowy Owls, perhaps the smaller, more agile males are more adept in aerial attacks on possible nest predators.

Females of some cavity-nesters, such as the Pearl-spotted Owlet and the Western Screech-Owl, flatten themselves on their eggs when disturbed at the nest. This behaviour presumably reduces the chances that the nest will be discovered by predators, but it exposes the incubating female to the risk of being killed in the cavity by the predator. Other species, such as Flammulated and Northern Saw-whet Owls, typically fly from the cavity before the intruder reaches the nest. Females of some of the open-nesting species, such as the Northern Long-eared and Short-eared Owls, characteristically defecate on their eggs when flushed from the nest by an intruder. Whether this behaviour is an attempt to make the eggs less appealing to predators, or is simply a consequence of the female having stored up a large amount of faeces while sitting on the nest, remains to be determined.

It is worth repeating that females of some species, notably Great Grey, Ural and Snowy Owls, once their young have hatched, can be extremely fierce when the nest is approached by a human

being; although the degree of hostility varies individually, some females will launch an attack when the intruder is still about 100 m away, and they are capable of inflicting very serious injury. Even after the owlets have left the nest, it is unwise to attempt to get too close to these owls.

Young *Aegolius* and some *Glaucidium* have their full juvenile plumage, and are reasonably adept at flying, as soon as they leave the nest cavity. Other young owls tend to leave the nest when still covered in down and unable to fly. Young Great Horned, Great Grey, Northern Long-eared, Short-eared and Marsh Owls typically move away from the nest, hopping or walking along adjacent branches or on the ground; these "branchers" enjoy high survival, and the move from the nest probably reduces the risk of predation. Young scops-owls and screech-owls are similarly downy and poor fliers when they leave the nest cavity, and they stay close to the nest-site for the first few days. Flammulated Owls can only glide when vacating the nest, but subsequently they can gain altitude by climbing up tree trunks, using the bill and feet.

In their study of the last-named species, B. D. Linkhart and R. T. Reynolds found that a brood would leave the nest over two consecutive nights. Within three days of the first young leaving, the brood had separated into two clear groups, one being fed exclusively by the male and the other by the female; the young in each group were those that left the nest on the same night. By dispersing young over a larger area, brood division may reduce predation in much the same manner as does "branching". No other direct evidence exists for brood division in owls, but very few studies have examined behaviour during the post-fledging period. J. R. Belthoff and G. Ritchison found no evidence that Eastern Screech-owls divide their broods, and J. Olsen and S. Trost determined that fledged broods of Southern Boobooks were fed by both parents for two to four weeks until the male took over all care.

For few owls has the fledgling period been studied, because of the difficulty of following individuals without using radio-telemetry.

During incubation, the female owl sits tight, leaving only occasionally, and for very brief periods, in order to defaecate and to eject pellets. Throughout this time she is fed on the nest by her mate, who is responsible for all the hunting during this stage of the breeding cycle, as well as during the brooding stage, which is also carried out by the female. Here, a male Great Grey Owl is feeding his incubating partner on the nest.

[*Strix nebulosa lapponica*, Sweden.

Photo: Bengt Lundberg/
BBC Natural History Unit]





Only limited information is available on the copulatory behaviour of the great majority of strigids, and for many nothing is known. It is thought that most copulations take place shortly after dark, but this probably does not apply to all species; moreover, the difficulties of observing and recording such activities at night are self-evident. Copulation is preceded by the male offering food to his partner, the latter usually making begging calls and movements similar to those of young owls. This pair of Brown Fish-owls is just about to mate.

[*Ketupa zeylonensis*
leschenault,
Corbett National Park,
India.

Photo: Gertrud &
Helmut Denzau]

The Flammulated Owl fledglings mentioned above became less dependent on the adults about three weeks after leaving the nest, and left the territory about one week after that, in late August. Juveniles of the larger species, such as the Spotted Eagle-owl, are dependent on their parents for a much longer period of time, perhaps as long as five months. The reasons for this long-term dependency are not clearly understood, but such periods may be important in long-lived species that hunt challenging prey. Studies of Eastern Screech-Owls have shown that juvenile dispersal is controlled by intrinsic factors, a "natal restlessness" similar to the migratory restlessness experienced by migrating birds. Parental aggression is apparently not important in the initiation of dispersal. Recent work on Eastern and Western Screech-owls by J. R. Belthoff and A. M. Dufty suggests that the steroid hormone corticosterone is the proximate mechanism that triggers such dispersal.

Large owls that are resident on the same territory throughout most of their lives tend to be long-lived. One Great Horned Owl survived almost 28 years in the wild, and Eurasian Eagle-owls also live longer than 20 years, whereas Barred and Tawny Owls have been known to live for more than 18 years in the wild. Medium-sized nomadic or migratory species such as Burrowing, Northern Long-eared and Short-eared Owls have much shorter life expectancies, more of the order of five to nine years, although one exceptional Northern Long-eared Owl survived for 27 years and 9 months. Western and Eastern Screech-owls have been known to live about 13 years; although small, both species are non-migratory. Small nomadic or migratory species such as Elf Owls and Northern Saw-whet Owls have the shortest natural lifespans, only four to seven years. In captivity, however, many of these owls can live much longer. For example, a captive Northern Saw-whet Owl died at the impressive age of 16.

Movements

The vast majority of owls show no patterns of movement outside their normal home ranges, other than juvenile dispersal. Fewer than 20 species, less than 10% of the Strigidae, have truly migratory populations, and in only half of these species is migration undertaken by a significant number of individuals. Nonetheless, owls demonstrate most of the strategies shown by birds, from

permanent residency to sporadic wandering or nomadism, partial migration and full migration. Migratory individuals move after the breeding season to a separate wintering ground, then return to the same breeding area in the following year. No species of owl, however, is completely migratory, where the entire breeding range is vacated in winter. Insectivorous species make up the bulk of true migrants, whereas species that specialize on cyclical rodent populations tend to undertake irregular nomadic or irruptive movements.

The few insectivorous owls that breed in northern temperate regions have fully migratory populations. For example, northern populations of the Brown Hawk-owl migrate from northern China, eastern Russia and Japan to Indonesia and the Philippines. They return to Japan each May, where they are the commonest owl in that country during the summer months, subsisting on a diet dominated by invertebrates.

The migratory pattern of the Oriental Scops-owl is similar, with northern populations moving from Mongolia, eastern Russia, northern China, Korea and Japan to wintering grounds in southern China and South-east Asia, where they mix with resident populations of the same species. Migrants often collide with lighthouses in the Straits of Malacca while flying from the Malay Peninsula to Sumatra. Apparently, there are only two confirmed records of the Oriental Scops-owl wintering in Sumatra, and none from Kalimantan, but individuals have landed on ships in the South China Sea, indicating a migratory path between Indochina and Borneo. Wintering numbers in Indonesia may be larger than the available data suggest, because these small owls would be very difficult to detect in forested wintering habitats, especially if not calling.

Similarly, there are extremely few winter records of the Flammulated Owl, a common species that breeds throughout the western cordilleras of North America north to central British Columbia, but retreats in winter to the pine-oak forest of Mexico and northern Central America. This lack of winter records led one ornithologist to suggest that this owl is able to spend the winter in a state of torpor, just like the similar-sized caprimulgid, the Common Poorwill (*Phalaenoptilus nuttallii*). Subsequent studies on the physiology of these owls, however, have ruled out this interesting possibility, so the difficulty of finding a small, silent, nocturnal owl in a relatively unexplored region is more likely the reason for the lack of winter records of Flammulated Owls.



One of the better-studied owls is the Little Owl, here shown copulating. The male of this species usually utters a brief call to attract the female for copulation, following which he may bob up and down in front of her before mounting; the female may crouch and shiver her wings, or the male may simply mount her without any preamble. During copulation, the male often grabs his partner's head feathers in his bill, while she holds her body in a horizontal posture. Copulation itself is brief and lasts only a few seconds, before the male dismounts. Allopreening appears to be important in the pre- and post-copulatory behaviour of many species, including the Little Owl, and it also serves to cement the pair-bond.

[*Athene noctua vidalii*,
Vallès Occidental,
Catalunya, Spain.
Photos: Oriol Alamy]

The Flammulated Owl's close relative, the Eurasian Scops-owl, migrates from Eurasia across the Sahara to central Africa, although some birds remain year-round in the Mediterranean area. Migration of individuals from higher latitudes is also illustrated by the Austral Pygmy-owl, whose breeding populations in southern Argentina move north in winter to sites in the northern half of Argentina. Similarly, the southernmost populations of the Southern Boobook show at least a partial migration to warmer areas of northern Australia in winter.

Migration patterns of other strigids are often obscured by the fact that the more northerly or, as is the case with one or two Southern Hemisphere examples, the more southerly breeders migrate to wintering areas already occupied by resident populations of the species concerned. The wintering grounds of Burrowing Owls breeding in the northern USA and southern Canada have long been a mystery. The birds move south in October and return in March and April, but, because they mix with resident populations in winter, it has been difficult to determine their whereabouts in that season. Recent radio-telemetry studies of Burrowing Owls that breed in the Canadian province of Saskatchewan have found a few birds wintering on the south coast of Texas and adjacent areas of north-eastern Mexico.

Perhaps the most migratory of owls, at least in terms of the proportion of the breeding population leaving the breeding grounds each year, is the Snowy Owl, which nests on Arctic tundra throughout much of the Northern Hemisphere. Most Snowy Owls leave their breeding territories each autumn, spending the winter in the taiga and plains of Eurasia, Alaska and Canada. A few individuals, reputedly adult males, winter within the breeding range, although the number probably varies widely from year to year. Snowy Owls also exhibit nomadic and irruptive movements. The variation in these movements is illustrated by three siblings ringed in 1960 in a nest on Victoria Island in the Canadian Arctic: one was recovered in October 1961 in eastern Ontario, Canada; another was found in May 1962 on the Hudson Bay coast; and the third was found in February 1962 on the island of Sakhalin in eastern Russia.

P. Kerlinger and M. R. Lein have studied these movements in North America and concluded that some, if not most, North American Snowy Owls migrate each year to winter on the Canadian prairies and, to a lesser extent, the northern Great Plains

of the USA. Wintering numbers west and east of the prairies are much more irregular: on the Pacific and Atlantic coasts, large numbers are found only in irruption years, with a preponderance of first-year birds. Populations on the Canadian prairies are dominated by adults, and immatures predominate farther south in the north-central USA. Among the birds regularly wintering in central North America, Kerlinger and Lein found that adult females remained farther north than the other age and sex classes, whereas immature males wintered the farthest south. They hypothesized that the large adult females were able to displace other birds and maintain winter territories closer to the breeding grounds through social dominance. How this situation relates to reports that adult males are more likely to remain on the breeding grounds is unclear.

Northern Hawk-owls are vole specialists, and breeding populations show distinct patterns of nomadism, vacating large areas in one year to breed in other areas of higher vole density in the next. After a peak in the vole population, the numbers of these owls can be very high in some areas. When vole numbers crash, the owls move out *en masse*, going south or to lower elevations in search of prey. I. Byrkjedal and G. Langhelle studied these classic irruptive movements in Norway, and found that adult females were much more likely to leave their breeding areas than were other age-sex classes, whereas adult males were more likely to remain on the breeding grounds. These movement patterns of males and females are more or less the opposite of those found in Snowy Owls, probably because it is advantageous for male Northern Hawk-owls to remain close to breeding territories that contain scarce tree cavities for nest-sites.

A proposed relationship between prey specialization, nest-site scarcity and migration strategy was put forward by A. Lundberg, who noted that owls specializing on small mammals with cyclical populations are more likely to be migratory or nomadic, whereas those nesting in scarce tree cavities are less likely to leave the breeding grounds. Thus, Snowy and Short-eared Owls prey on voles or lemmings, nest on the ground, and show a high level of nomadism, whereas Ural and Barred Owls have broader feeding niches, nest in large tree cavities, which are scarce in their breeding ranges, and are year-round residents on their territories. Boreal Owls, which nest in tree cavities and feed on voles, show an intermediate pattern, with adult males remaining on the



Once the chicks have hatched, the female owl broods and protects them continuously until they are big enough to be left on their own for short periods without the risk of losing too much body heat. She tends them with great care, feeding them with items delivered by the male. In many strigids, including the Short-eared Owl, the defence of the nest is undertaken largely by the female; as she is usually larger than the male, and is frequently alone at the nest, this is perhaps not surprising. The male occasionally assists if he happens to be nearby, but male Short-eared Owls can also be very aggressive towards intruders, making diving attacks and sometimes drawing blood.

[*Asio flammeus flammeus*, Great Britain.
B. Speake/Aquila]

breeding territories all year round and females and young birds dispersing from their breeding and natal areas, respectively, at least during years of vole scarcity.

The dispersal and migration strategies of Boreal Owls have been well studied in Germany and Finland. Prey populations in Germany are much more stable than those in Finland, where vole numbers are highly cyclical. Boreal Owls in Germany, therefore, tend to remain on the breeding territories throughout the year, whereas those in Finland are much more prone to leave their territories after breeding during periods of low vole numbers. Female Boreal Owls from both areas move more often between breeding seasons, and travel longer distances, than do adult males. Because the smaller, more agile males can probably catch a wider range of prey, they can make a living on their breeding territories even when vole populations are very low.

The Northern Saw-whet Owl is another species with a partial-migration strategy. This species winters throughout its breeding range, but considerable numbers of individuals from northern populations move south in winter, some covering thousands of kilometres from central Canada to the central USA. Each year, between 2000 and 5000 of the owls are ringed at trapping stations in the USA. In most years, the bulk of this movement applies to young birds, but many adults migrate as well. Populations migrating along the Atlantic coast of the USA are dominated by juvenile females, and adult males are the least common age-sex class encountered. Ratios of juveniles to adults vary from 10:1 in irruptive years to 1:4 in years when few birds migrate. Some individuals have been recaptured at the same ringing stations in subsequent years, suggesting that the same migration routes are used regularly by some owls.

Northern Long-eared Owls have a stronger tendency to migrate out of northern breeding areas than do Boreal and Northern Saw-whet Owls. They are probably more sensitive to snow depth than the latter two species because they prefer to hunt over open fields, which are more prone to accumulate snow than are the forests where Boreal and Northern Saw-whet Owls search for prey. Their favourite nest-sites, stick nests built by corvids and hawks, are probably more readily available than are suitable tree cavities, so there is less pressure for male Northern Long-eared Owls to remain on territories at the northern edge of the species' range.

The seasonal movements of owls that breed in mountainous areas are often vertical (in elevation) rather than latitudinal. In winter, Great Grey Owls in Oregon, USA, move to lower elevations that have less snow than their breeding territories and, also in western North America, Northern Pygmy-owls routinely move from montane forest to valley bottoms, where they feed on passerines that congregate in winter at suburban bird-feeders. Conversely, Spotted Eagle-owls in Malawi move to higher, cooler elevations during the hottest months of the year.

Owls with nomadic habits often fly large distances, sometimes hundreds of kilometres, to new breeding sites, usually when prey populations at their previous sites have crashed. Snowy Owls, Northern Hawk-owls and Short-eared Owls are good examples, but Great Grey, Boreal, Northern Saw-whet and Northern Long-eared Owls also have nomadic tendencies. When vole populations crash in the northern forests, Great Grey Owls abandon their territories and wander widely in search of better hunting conditions; the female of a pair will usually move first, then the male too if conditions remain poor. Similarly, of 23 Boreal Owl males studied in Finland by E. Korpimäki and associates, most moved less than 1 km and none moved more than 5 km between breeding sites, whereas half of the adult females moved more than 4 km and one shifted 580 km. Southern White-faced Owls and Marsh Owls are also somewhat nomadic in the drier parts of their ranges, appearing in numbers after rains have produced an abundance of prey and, in the case of Marsh Owls, tall grass for nesting. Pel's Fishing-owls make irregular movements, stimulated by droughts that render their breeding territories unsuitable.

Nomadic species also have irruptive tendencies: not only do they wander widely in search of good foraging areas, but they also periodically invade regions in large numbers. Often, these latter areas are not part of the species' normal breeding or wintering range. This phenomenon is generally thought to result from high populations produced during times of prey abundance, usually related to the vole population cycles in northern forests. When prey populations plummet, the large number of young owls produced during the vole peak, and many of the adults as well, are forced to disperse to find food. A dense population of Short-eared Owls studied by A. Village dispersed widely after a significant spring decline in vole numbers in southern Scotland; an adult male was found dead in southern England in November, and in

This male Snowy Owl, having succeeded in catching a large rodent, is delivering it to the female, so that she can prepare to pass the meal to the nestlings. When the young owls are older and able to manipulate sizeable prey themselves, the male may drop food items at the nest, or even transfer them directly to the young.

[*Nyctea scandiaca*,
Greenland National Park,
Greenland.
Photo: Jean-Louis Klein &
Marie Luc Hubert/Bios]





In the case of species which nest in tree holes, the young, when old enough to stand comfortably, will come to the entrance of the hole to receive food from the arriving parent. These young African Wood-owls are well advanced in their growth and development, and are able to stand at the opening of the nest to take prey items from the incoming adult. The latter generally announces its imminent return with a special call, recognized by the owlets.

[*Strix woodfordii woodfordii*, Somerset West, Western Cape, South Africa. Photo: J. J. Brooks/Aquila]

December an adult female was shot in Spain, 1730 km south of its breeding territory. In the following spring, others from the same population appeared farther north, in the Shetland and Orkney Islands. A juvenile male Northern Long-eared Owl, dispersing after a vole crash in Saskatchewan, Canada, was killed in Oaxaca, Mexico, in the same year, having made a journey of almost 4000 km. Two others of that species ringed in the USA, one in Minnesota and the other in Montana, were recovered in Mexico more than 3000 km from their respective ringing sites.

Of course, juvenile dispersal is characteristic of all strigids. Distances covered are relatively short in some species, but they can be very long in others. Juvenile Spotted Owls in New Mexico, USA, dispersed over distances ranging from 1.3 km to 145 km, some crossing wide areas of unsuitable habitat to different mountain ranges. J. R. Belthoff and G. Ritchison found that Eastern Screech-owls in Kentucky dispersed up to 16.9 km from their natal territories, with a median value of 2.3 km, but the authors were unable to differentiate the sexes in their sample. In Finland, however, E. Korpimäki and associates found that juvenile female Boreal Owls dispersed farther than did juvenile males, with median values of 80 km and 20 km, respectively. Of 189 Northern Long-eared Owl fledglings ringed by J. S. Marks in south-western Idaho, four were captured as breeders a year later; all were males, and each bred successfully 50-1500 m from its natal nest, demonstrating that, even among "nomadic" species, juvenile dispersal can be exceedingly short in some cases.

Examples of what may be considered true vagrancy by strigids are understandably few. Nevertheless, Northern Hawk-owls of the North American subspecies *caparoch* have been identified in Britain and on the Canary Islands. In addition, there are several records of Eurasian Scops-owls and Boreal Owls in Britain, far outside the breeding range of either species.

Relationship with Man

Owls have held a special fascination over humans for thousands of years. With their large eyes positioned on the front of the head and, in some cases, with "ears" that appear to be in the right place, the strigid owls have a human-like quality that many people find irresistibly endearing. At the same time, however, the

human-like appearance of owls, combined with their nocturnal habits and haunting vocalizations, invoke fear and superstition among people of many different cultures. As a result, owls have been inseparably linked with death wherever they occur.

It is highly likely that owls were among the first birds to play an important role in the legends and myths of ancient man, probably because their vocalizations in the dead of night could have caused havoc in the superstitious mind. Because humans undoubtedly evolved in Africa, it must be there that the paths of owls and human beings first crossed; yet, the first "written" evidence of contact between humans and owls comes from Europe. Some 15,000 to 20,000 years ago, Upper Paleolithic people in southwestern France painted the first known owl interpretations on their cave walls. A simple rock painting, discovered in December 1994 in La Crotte Chauvet cave, illustrates an owl with ear-tufts, making it either a *Bubo* or an *Asio*, or perhaps an *Otus*.

At the Trois-Frères cave in the French Pyrenees, another ancient painting depicts a curious figure of a man with antlers. Experts in prehistoric art named it the "Sorcerer". The subject's erect posture identifies it as a human, but the rest of the body is a mix of non-human animal parts, including the head of a crow, the face of an owl, the ears of a wolf and the beard of a chamois. The "Sorcerer" is most likely a shaman who is performing a dance to ensure the success of an imminent hunting excursion. By depicting the face of an owl, the artist might have been striving to endow the hunter with excellent eyesight, especially in darkness.

Aboriginal cave paintings demonstrate that owls have fascinated humans for millennia in Australia, too. "Dumbi the owl" was the son of a Wandjina, which is a half-human spirit that Aborigines believe existed at the creation of the world. A long time ago, the young Dumbi was pulled from his nest by some boys, who tore off his feathers, maimed him with a stick, and threw stones at him. When he learned of the boys' cruelty, the Wandjina called in a voice like thunder and sent lightning and rain on the place. Many people drowned in the flood that ensued, which is why the children never touch owls today.

In other parts of Australia, owls were thought to guard the souls of women, a belief that gave them a measure of protection. Each woman believed that the lives of her mother, sisters, daughters and so forth, and equally her own life, were bound up with

A further example of the adult feeding its well-grown chicks directly is provided by this Little Owl at its nest in an old orchard. As with the passing of food from male to female, prey items are presented to the chick bill to bill. Several studies have revealed that the nestlings of this species can climb up to the nest entrance when about three weeks old, and that they receive frequent food deliveries from the parents. Young Little Owls, like those of many strigids, often venture outside the nest before they are capable of flight, which in this species occurs at 30-35 days of age.

[*Athene noctua vidalii*,
Warwickshire, England.
Photo: Mike Wilkes/
Aquila]



the lives of particular owls and that, in guarding the owl species, she was guarding the lives of her female relatives. In parts of Asia, the owl was considered a protector, a divine ancestor, who helped ward off evil spirits, famine and pestilence. In the Pacific islands of Samoa, people believed that they were descended from an owl, although it is not known which particular species their ancestor was supposed to have been.

The family name Strigidae, and the generic name *Strix* to describe a large number of species, suggest an undeservedly sinister reputation among owls in general. *Strix* is Greek for "witch", being transformed to *striga* in Latin; naturally there is no reason to believe that the 19 species of *Strix* are any more likely to be associated with sorcery than are the other owl species. Nevertheless, the conviction that all owls are linked with witchcraft has been widespread throughout the world.

In Sicily, for example, legend has it that, if a Eurasian Scops-owl called near the house of a sick man, he would die three days later. If nobody nearby was sick, then the owl's call announced that someone would be struck down with tonsil trouble. To the Chinese, owls snatched away souls, and their calls were referred to as "digging the grave". In the Arab world, it was believed that owls were the souls of people who had been killed. In Hispaniola, Stygian Owls were persecuted by local people who believed that owls had supernatural powers and could transform themselves into witches. Indian tribes living on the pampas of Argentina feared the Burrowing Owl, and their name for the species translated to "sister of evil"; reportedly, they killed every Burrowing Owl they encountered, and would not make camp in areas where these owls had nested. Elsewhere in American Indian culture, owls were thought to possess mysterious powers and were widely believed to presage the death of people who heard them and to bring illness upon people deserving of such fate. The Pima Indians of the south-western USA believed that the owl could safely guide them on their journey from life to death. By Pima custom, an owl feather was placed in the hand of one thought to be near death, in the belief that the owl would know that the person was ready to embark on the journey; the feather had to be one that was moulted by a living owl, and the Pimas collected such feathers whenever they found them. Indeed, Pima shamans sometimes kept live owls, taken as nestlings, for the purpose of building up a stock of appropriate feathers.

In Africa, especially, it is still commonly alleged that these nocturnal birds are possessed demons. Consequently, to see one is a sure sign of impending disaster, more so than walking under a ladder or seeing a black cat cross the road. Witchdoctors in West Africa are required to mingle their own blood with that of an animal during the blood-brother initiation. Although the bond is usually established with a ferocious creature such as a leopard.

A most interesting aspect of owl behaviour is demonstrated by this adult Morepork. Having returned to its nest with a tasty morsel of food, it does not offer this directly to its young waiting at the entrance. Instead, it perches very close by, attempting to encourage the owlet to leave the hole. The young of many species of strigid habitually leave the nest before fully fledged, and remain nearby in the surrounding branches; this behaviour, known as "branching", is thought to reduce the risk of the entire brood being preyed on.

[*Ninox novaeseelandiae*
novaeseelandiae,
Katikati, North Island,
New Zealand.
Photo: Brian Chudleigh]





Even after the young have left the nest, the parents' duties are far from over. The owlets remain dependent on their parents for several weeks or, in the case of larger species, even some months after they have fledged. Here, a female Austral Pygmy-owl is feeding a mouse to its offspring, which have clearly left the nest hole for the last time. Although the period of post-fledging care of this species is not known for certain, it is likely to be at least three weeks. During this time, the young owls will learn to catch their own food and to fend for themselves.

[*Glaucidium nanum*, Torres del Paine National Park, Chile. Photo: Günter Ziesler]

snake or crocodile, owls and other night birds are acceptable alternatives.

In South Africa, owls were believed to be sent by evil witchdoctors to kill people. Should an owl settle on a hut, it was regarded as a messenger of death; even if it merely screamed while flying over the hut, it was believed to be foretelling some misfortune to the inhabitants. Not surprisingly, people threw burning brands at the birds to drive them off. If the owl was caught, it was soaked in paraffin and set on fire, possibly to break the witchdoctor's evil spell. South African tribes maintained that one must not imitate the cry of an owl, lest one's blankets be burned. In Madagascar, owls were said to join witches as they danced on graves. If an owl was captured in West Africa, its claws were broken and it was otherwise mistreated in the belief that the witchdoctor who sent it would suffer the same pain; in Nigeria, the owl was so dreaded that people would not mention it by name, referring to it instead as "the bird that makes you afraid". Furthermore, in Morocco, small children were not allowed to play outside after dusk, because it was believed that an owl flying over would make them seriously ill.

Some cultures also have stories of man-eating owls whose diet consists primarily of small children. In parts of China and Malaysia, it has been held that owls are particularly partial to the blood of newborn babies, and several North American Indian stories tell of children being taken away and eaten by these birds.

Recent comparative studies into different parts of the world demonstrated that many more superstitions about owls still exist in Africa than in Central America. In Malawi, more than 90% of the 147 people interviewed connected owls with bad luck, witchcraft and death. In Costa Rica, however, only 4% of 162 respondents associated owls with bad omens, and an additional 3% listed them as "frightening". In Chiapas, in southern Mexico, 102 students between eleven and 20 years of age were interviewed in 1998, and 17.6% stated that owls are birds of bad luck; on the other hand, an equal percentage considered them to be beneficial. A British television survey similarly interviewed more than 300 people aged 15 and older about their animal likes and dislikes. When given a choice between the terms "frightening" and "non-frightening", 39% of the respondents considered owls to be frightening, 35% did not, and 26% preferred to view owls as neither.

One possible explanation for these strong superstitions in the twentieth century is that owls are frequently associated, correctly so, with cemeteries. For example, where heavy deforestation has occurred near villages in Malawi, graveyards are often the only wooded areas remaining in the landscape, so that owls, naturally, use them for breeding and roosting. As people encounter owls more and more often in such places, the belief that the birds are connected with death is reinforced. Elsewhere, strigids that inhabit old-growth and mature forest may be associated with sacred large trees in riparian gallery forest, near temples and in cemeteries. In India, the Forest Eagle-owl plays a major role in many legends and is said to be associated with Hindu cemeteries, which are often the only local bastions of old-growth forest with large trees and snags. Forest Eagle-owls, Brown Fish-owls and Brown Wood-owls (*Strix leptogrammica*) also inhabit gallery forest of *Ficus* near water-holes and streams in India, which are sacred temple areas. In a sense, then, many of these species serve as indicators of the religious value of a forest. It is likely that the Sunda Scops-owl has survived in Java only because of the ill omen or reverence it represents in Indonesian legends.

Superstitions die hard, and all too often they give rise to behaviour quite disproportionate to an alleged offence. In Malawi and in East and South Africa, 189 people interviewed had witnessed 51 killings of owls. They listed the reasons for the killings as follows: superstitious beliefs to avoid bad omens (27.5%); just for fun during hunting (19.6%); to be eaten as a relish (15.7%); because the owl made too much noise (11.7%); to make magic medicine (7.7%); because it was nesting too close to a house (5.8%); because of the association with witchcraft (2.0%); because the owl killed a hen, attacked first, entered a hospital, or was killed by a car (each 2.0%); and for reasons unknown (2.0%). The overall picture provided by this survey is that little mercy is shown to owls in much of Africa.

In other cultures, the owl has appeared on artefacts such as Peruvian Moche pottery jugs, and North American Indian pipes and shields, and in delicate Chinese and Japanese paintings. In the past, owl symbols were used simply as signs of good luck, but today they appear in connection with anything from reading glasses to computers. At least two professional football clubs in England use the owl logo. Cigar boxes made by the White Owl company feature a Snowy Owl and have become a familiar sight

A steady supply of food is of vital importance for growing owl chicks, and the majority of strigids therefore time their breeding to coincide with the period when their preferred prey animals are most numerous and most easily accessible. Many owls breeding in the far northern parts of the globe are to a large extent dependent on voles.

With abundant food at hand, the well-fed females are more likely to produce large clutches, and the resulting offspring will also have a greater chance of survival. A good example is provided by the Snowy Owl. Pairs of this species breeding on tundra are almost totally dependent on lemmings and other voles, both as food for themselves and as food for their young. This youngster has been presented with a Norway lemming (*Lemmus lemmus*), a staple dietary item of Snowy Owls in Scandinavia and throughout the range in which that rodent occurs.

When lemmings are abundant, the female owls will lay clutches of as many as eleven eggs, with high fledging success. In years when lemming populations crash, other voles will be exploited. In years when no vole species are available in sufficient number, however, the risk of expending a great amount of energy in breeding, only to fail because of an inadequate food supply, is so great that these owls will forgo all nesting attempts for that season.

[*Nyctea scandiaca*,
Sweden.

Photo: Tony & Elizabeth
Bomford/
Oxford Scientific Films]



in the USA. That same species has also been depicted on the \$50 note in Canada since 1988.

Since ancient times, owls have been regarded as symbols of wisdom. They have been portrayed on coins, medals and books, and have even been associated with libraries and universities. Perhaps the best-known example of this symbolism is that concerning the Little Owl and the Greek goddess of wisdom, Athene; in ancient Greece, Athene was allied with the sacred owl of Athens, which now carries the generic name *Athene*. A Little Owl was depicted on a coin in about 450 BC in Greece, where its name was virtually synonymous with money, and a Little Owl coin also was minted in conjunction with the 350-year anniversary of the University of Helsinki in Finland.

No self-respecting gift shop in the Western world is without a display of owls manufactured in a variety of materials, from shells, glass and metal to minerals, pottery, wood and even polished coal, and a number of businesses have adopted the bird as a company logo, believing it to be a sign of integrity and wisdom. Thousands of people have lately become "addicted" to owls and collect anything with an owl on it. Most of the "owl aficionados" live in Europe and the USA, but such people also abound in South Africa, Australia and Japan, and even less "westernized" places such as the Philippines and Fiji can claim a few avid collectors of owl souvenirs. Serious "owlaholics" admit that they sleep on owl sheets, hang their toothbrushes on owl-shaped stands, dry their hands on owl towels, cook with owl oven pads, and wear owl jewellery. Most collectors, however, merely accumulate owl figurines, carvings, statues and paintings, while matchboxes, greeting cards, stamps and postcards with an owl on them are also very popular collector's items.

Night-shift workers and those who love the night-time hours inevitably are known as "night owls", who spend their time "owling" around. In the light of this, it is interesting to note that in Italy, particularly in the city of Bologna, a policeman on the beat is known as a "*gufo*" owl, and all over Italy the word "*civetta*", which means small owl, is used to describe a police patrol car.

Ghostly forms and weird, hooting cries of owls have inspired conflicting emotions, ranging from terror to reverence. Directors of horror and action films often add the call of a Tawny Owl to soundtracks at tense moments, and with good reason: this species' call must surely be one of the most evocative sounds in nature for many people. In viewing movies, one could easily get the impression that Tawny Owls are common in the USA, al-

though they occur only in the Old World! Similarly, the rapid staccato song of the male Boreal Owl can be heard in many movies during night scenes filmed far outside the species' geographical range, and always in the wrong habitat!

Owls have even found their way into *haute cuisine*. The Creoles of Louisiana, USA, perhaps inheriting dishes from French cuisine, used to eat Barred Owls. The hunting of Snowy Owls for food or other purposes seems to have been an old tradition that continues to some extent among Eskimos, who describe these owls as "lumps of fat". During the last glaciation, large numbers of Snowy Owls were eaten and used for magical purposes. Cave deposits in France have yielded thousands of bones of this species, often representing hundreds of individuals, and up to 90% of all bird bones collected. Some restaurants in China still have owls on the menu as great delicacies; one such is near Dan Xia Mountain, from where the local people catch wild animals, including owls, which they sell to local restaurants in the city of Shao Guan. In Uruguay, the flesh of the Burrowing Owl is served as a delicacy to local people convalescing from illness, in the belief that it produces an appetite for other foods.

Not everybody finds owls agreeable from an epicurean standpoint, but parts of owls may be consumed in the conviction that they have magical powers. A general belief in Africa has been that eating an owl's eye improves night vision. In North Africa, it is said to be essential to know which eye to eat, for an owl sleeps with one eye closed and the other permanently "awake"; to tell which is which, the eyes must be placed in a bowl of water, where the sleepy eye will sink and the desirable one will float. In Morocco, suspicious husbands and fathers had a rather different use for owl eyes, and one that did not even depend on the co-operation of the wife or daughter: placing the right eye of a Eurasian Eagle-owl into the hand of a sleeping wife or daughter ensured that the woman would tell the man exactly what she had been doing during the day.

Rather than using the owl as lie-detector or eating it, South African Bantus had a saying that owl flesh is not eaten, for its body is full of scurf that causes it to smell as if it were dead. In a more mundane context, a traditional saying exists in Yorkshire, England, to the effect that nice owl soup, presumably in moderate doses, is an excellent remedy for whooping cough. "Owl's-egg soup" is commonly reckoned to be effective against epilepsy, the only snag being that it has to be prepared when the moon is on the wane. In addition, owl eggs are seen as an effective cure



The breeding success of owls depends on several factors, among them food supply, weather conditions and levels of predation. The Burrowing Owl, since it nests in underground burrows, would seem especially vulnerable to predation of its eggs or young. This species lays 6-11 eggs, so this particular adult, photographed with young at its nest-burrow entrance in Canadian grassland, can be considered to have achieved excellent fledging success on this occasion. As owls normally raise only one brood per year, failure can have a serious effect on the total population.

[*Athene cunicularia hypugaea*,
Wardlow,
southern Alberta, Canada.
Photo: Duane Sept]



Having left the nest, juvenile owls feed avidly and, like the adults, swallow prey whole.

Mice can form a large part of the diet of the Northern Long-eared Owl and, with a good supply of these and similar rodents, the young fledgling grows quickly. This species can fly when about 35 days old, but is cared for by the parents until it is at least two months of age.

Parts of the downy mesoptile plumage are still visible on this juvenile, but will disappear by the tenth week or thereabouts.

[*Asio otus*,
Dachau,
southern Bavaria,
Germany.

Photo: Alfred Limbrunner]

for various kinds of excessive indulgences, notably that of heavy drinking, for which it is maintained that even one egg is sufficient to clear the head. Similar prescriptions claim that owl eggs cooked in wine for three days will cure the worst cases of drunkenness; this is easy to believe if the drunk himself boils the egg for three days.

Puerto Rican folklore states that the Puerto Rican Screech-owl feeds on coffee beans and that it can be used as a cure for asthma; the asthma cure must presumably involve eating the owl, but the source provided no details to that effect. Owls are also used as healing medicines in South America and Asia. In China, dried bodies of Collared Scops-owls serve as medicine for various illnesses, and such practices are even more prevalent in Korea, where large numbers of these birds are killed each year for this purpose. Thailand also has a large Chinese community, and body parts of owls feature in traditional Chinese medicine; many strigids, therefore, are destroyed for medicinal purposes in Thailand. In India, owls are used to treat various ailments such as nervous debility, body pain and similar problems. An old Indian belief was that the meat of an owl is a potent aphrodisiac, but in other places owl meat was thought to cause loss of memory or complete insanity!

The American hero of Alamo fame, Davy Crockett, was said to imitate the cry of the Barred Owl when hunting Wild Turkeys (*Meleagris gallopavo*), for the birds would invariably react by gobbling in response, thereby disclosing their whereabouts. The Ainu people of northern Japan, who also depended on hunting for their livelihood, used to drink a "toast" to Blakiston's Eagle-owl, which they considered to be a divine ancestor, before setting out on a hunting expedition.

Eurasian Eagle-owls, Tawny Owls and Little Owls are commonly used as decoys to catch corvids, and even songbirds, which are illegally shot for sport. Eurasian Eagle-owls have also been used as bait, fitted up with netting, to catch falcons and hawks, which are subsequently trained for falconry. Today, the technique has been brought up to date by bird-ringers and photographers interested in capturing or photographing mobbing birds that are

aroused by a live or stuffed owl. A Great Horned Owl tethered near a nest has been employed for catching Hen Harriers (*Circus cyaneus*) and Merlins (*Falco columbarius*), and a plastic decoy of that large strigid can be effective for netting Northern Long-eared Owls near their nests; as the parents swoop at the "trespassing" owl, they collide with mist-nets strategically placed around it. Even Ospreys have been caught using a captive Great Horned Owl tethered to a floating timber platform.

A couple from Queensland, Australia, have come up with a novel way of deterring cormorants from eating up their profits. The Butlers, who farm Australian prawns, have placed plastic owls around their property to keep away some 30 cormorants that regularly occur in the vicinity; they concluded that the owls protected the prawns, and even prescribed the treatment of two decoy owls per hectare of prawn pond. In North America, plastic decoy owls are widely used in attempts to keep Rock Doves from roosting on public buildings, although the doves invariably figure out the ruse in a short period of time. As a result, plastic owls bearing conspicuous white stains can be seen "perched" on roof tops and building ledges from coast to coast in the USA.

Some owls, especially Snowy and Short-eared, have become a problem at airports, where the relatively undisturbed fields surrounding such sites offer ideal habitats for mice and voles. Unfortunately, these same owls sometimes collide with aircraft, causing serious damage to engines although, so far (touch wood!), no fatal accidents. Luckily, trained eagles can be used to harass smaller birds, including owls, and thus help to prevent collisions with the planes.

The potential ability of owls, be they tytonids or strigids, to depress rodent numbers and other populations of pest species has been appreciated in many parts of the world. Farmers have built "owl holes" into the eaves of their barns and placed nestboxes in fields and forest to encourage owls to nest. In Kenya, tame owls have been used to hunt longhorn beetles that attack the trunks of planted *Casuarina* trees; owls were said to end the beetle invasion in short order. Moreover, and thanks to the recent efforts of conservationists, many rural people in the USA and



The populations of many owls are being reduced as a result of the disappearance of forest. This problem is particularly acute in the Philippines, where forest destruction has continued unabated for some decades. The Philippine Hawk-owl tolerates a moderate degree of habitat alteration and remains fairly common locally. The subspecies occurring on Mindoro, for instance, is common within the largest forest remnant left on that island, over 90% of which has been deforested. This race is considered by some to be a full species, and this photograph is probably one of the first taken of this form.

[*Ninox philippensis mindorensis*, Sablayan, Mindoro, Philippines.
Photo: Pete Morris]

Canada, as well as in Europe, have been enlightened to the fact that having an owl on one's property is beneficial.

Among the owls identifiably mentioned in the Old Testament of the Bible are the Eurasian Eagle-owl and the Tawny, Hume's, Little, Northern Long-eared and Short-eared Owls. Jewish people believed that owls were unwholesome because they ate raw meat and carrion and chose to live in derelict and desolate places. Aristotle, who lived from 384 to 322 bc, almost certainly was the first scientist who studied owls, among so many other things. For instance, the antagonistic relationship between owls and crows was mentioned in his book *Historia Animalium*.

Since the time of Aristotle, owls have been admired by scholars, artists and poets. A famous owl painting is that of Albrecht Dürer: reproductions of his 1508 painting of a Little Owl are owned by many owl-collectors and also appear on postcards and in books. Even Picasso painted an owl, an abstract figure that resembles a strigid and is dated to March 1957.

Owls have also figured prominently in English literature, as any lover of Shakespeare well knows (see page 60). For Shakespeare, the owl was clearly a bird of ill omen. In the nineteenth century, the Italian writer Giuseppe Gene wrote that the owl is very beneficial because it preys almost exclusively on vermin and is thus an ally to the farmer. In this light, Gene attacked, among other things, the barbaric custom almost everywhere in Europe of nailing an owl's carcass to the door of a house or barn, an act stemming from the erroneous belief that owls commonly killed farmyard animals or domesticated birds such as doves. He also pragmatically opposed the myth that perched and calling owls are messengers of death; according to Gene, an owl is just as likely to settle on and call from a house in which the occupants all enjoy the best of health, and it should, therefore, be seen as an omen of good fortune.

Owls were also a popular subject in the "nonsense" writings of Edward Lear in the nineteenth century. In the 1830's, Lear became one of the world's greatest bird-painters, and he had a special fascination with owls. His depiction of the Eurasian Eagle-owl in John Gould's *The Birds of Europe* (1832-1837) is today the most famous and sought-after plate among the 3000 illustrations produced in Gould's works. Sadly, Lear quit ornithological illustration in 1837, but he never forgot his beloved owls. In the limerick *Old Man of Dumbree*, Lear wrote:

There was an old man of Dumbree,
Who taught little owls to drink Tea,
For he said, "To eat mice
Is not proper or nice",
That amiable Man of Dumbree.

The Eurasian Eagle-owl may be the model for Lear's *The Owl and the Pussycat*, written in 1868 and published two years later:

The Owl and the Pussy-Cat went to sea
In a beautiful pea-green boat.
They took some honey and plenty of money
Wrapped up in a five-pound note.
The Owl looked up to the stars above,
And sang to a small guitar,
"O lovely Pussy, O Pussy my love!
What a beautiful Pussy you are –
You are;
What a beautiful Pussy you are."

Pussy said to the Owl, "You elegant fowl,
How charmingly sweet you sing!
O, let us be married – too long we have tarried –
But what shall we do for a ring?"
They sailed away for a year and a day,
To the land where the bong tree grows;
And there, in a wood, a Piggy-wig stood –
With a ring at the end of his nose,
His nose;
With a ring at the end of his nose.

"Dear Pig, are you willing to sell for one shilling
Your ring?" Said the Piggy, "I will."
So they took it away and were married next day
By the Turkey who lives on the hill.
They dined upon mince and slices of quince,
Which they ate with a runcible spoon;
And hand in hand, on the edge of the sand,
They danced by the light of the moon –
The moon;
They danced by the light of the moon.

Exploitation and "tidying" of forest means that fewer old trees and fewer holes are left for owls to nest in.

Since many owl species are reliant on tree cavities for breeding and roosting, the loss of so many sites is potentially very serious.

A particular case involves the Boreal Owl. This owl

nests mostly in old woodpecker holes,

predominantly those built by *Dryocopus* species,

and its habitat therefore has to contain trees of the

size preferred by those woodpeckers. In many

parts of its range, the removal of these trees has

created a major problem for the owl. One way in

which man has been able to help is by providing

artificial nestboxes, and such action has

proved highly successful. In Finnish forests, where

the large trees favoured by Black Woodpeckers

(*Dryocopus martius*) are now rare, about 95% of

Boreal Owls nest in boxes designed specially for them. Here, an adult

Boreal Owl is arriving at its nest inside an old

Norway spruce (*Picea abies*), carrying a wood

mouse (*Apodemus sylvaticus*); the young are

about 27 days old, and will leave the nest within a few

days. The plumage of the owlets at fledging is of

interest, being very different from that of the

adults: the juveniles are almost wholly chocolate-

brown, much as shown in this photograph, and the

young will not acquire adult-like plumage for

three months or more.



[*Aegolius funereus*
funereus,

Haute Ardenne, Belgium.

Photo: Serge Sorbil]

A further excellent example of the owl in literature is *Lady Grayl: Owl with a Mission*, written by R. W. Nero in 1994. This book is a kind of love story between the author and his tame Great Grey Owl. Nero took his beautiful "girlfriend" to countless schools and public meetings in Canada to "preach the gospel of conservation". Using his own words as an example: "Nowadays I find myself interacting with Grayl as if she were more than a bird, as if she could understand me. It's silly, but there is some sort of relationship between us, such that she greets when I come to her pen, a soft cooing or humming sound. I either reply in kind, or speak directly to her." Also included in Nero's book is the following poem, *The Owl's Gift*:

In the dark rainy night
I consult with this oracle
reaching through soft feathers
to feel her warm throat
thinking as I do that
the fabric of her being
is mere thin skin stretched
over braced bones and flesh
a fragile assemblage
to so command our attention.

So then where's the spirit of
this comforting creature that
ceaselessly charms us all?
It must be in her mind
(do birds have minds?)
It's in her attitude, the way
she trusts us and accepts us;
she comes from her owl-being
to meet us in her time
gravely allowing us a
glimpse of her world
a gift of tender tolerance
we do well to honour.

During the last 30 years or so, the keeping of captive owls for rehabilitation and breeding purposes has become very common in Britain, Germany, France and the USA. Many of the 500 or more captive-breeders are serious conservationists who strive to help the diminishing wild populations of rare species. Some facilities are strictly for keeping owls for rehabilitation and study, whereas others include educational programmes. Without question, well-organized demonstrations can add to the general knowledge of owl biology, without which conservation efforts would not be successful. Unfortunately, some of the owners are keen only on making money from selling owls, or they seem to obtain rather dubious satisfaction from having a collection of rare owls in captivity. The International Owl Society (IOS) is a serious effort to advise owl-keepers by grouping them together and sharing information through the society's magazine, *Tyto*. The IOS stresses the fact that in Britain it is an offence to sell, or to offer to buy or sell, most wild birds, dead or alive, without a licence or exemption from the Department of the Environment, or, in the case of dead birds only, registration under the Wildlife and Countryside Act 1981. Although these conditions apply in Britain, it is worth remembering that similar rules and acts are also in place in most countries of the world.

Status and Conservation

It should come as no surprise that information on the status and ecology of most strigid populations is woefully incomplete. This fact has important implications for conservation, because it is difficult to safeguard a species without a thorough understanding of its ecology. On balance, humans have exerted a negative influence on owls, as they have on most groups of birds, and, despite the recent upsurging interest in bird conservation, the situation is likely to get worse before it gets better. Part of the problem is that the largest numbers of strigid species inhabit areas of tropical forest, and these are being ravaged at a rapid pace.



Habitat degradation, coupled with subsistence-hunting, has led to a huge decrease in the population of the Philippine Eagle-owl. Although one was reported in 1994 from Bohol, where the species had never previously been recorded, there are very few recent records of this magnificent species, and all of those are from Luzon, where this captive individual was photographed. This eagle-owl is one of a number of Endangered species inhabiting the islands.

[*Bubo philippensis*,
Manila, Luzon,
Philippines.
Photo: Clifford &
Dawn Frith]

In addition, many species are endemic to islands and therefore have small population sizes and restricted geographical ranges, making them vulnerable to habitat alteration and other unnatural factors that could increase predation risk, destroy scarce nesting sites and reduce food availability. Further, because of the difficulty in determining species limits, especially in the tropics (see Systematics), an undetermined number of species yet to be formally recognized can almost certainly be considered in peril, unbeknown to scientists and conservationists. The sad conclusion of these factors is that several species of owl are likely to disappear before we have learned even the most rudimentary aspects of their biology.

That owls endemic to islands are highly vulnerable to extinction is reflected by the fact that each of the taxa thought to have become extinct in the last 300 years inhabited islands. Tracing the history of these extinctions is difficult, because most of the taxa disappeared before scientists had viewed them in the field. For example, the physical evidence for the occurrence of two strigids on Rodrigues Island, in the Indian Ocean, consists only of bones. The Rodrigues Little Owl (*Athene murivora*) was described from a tibiotarsus and a mandible. Its presence was also supported in an anonymous manuscript located in Paris and entitled *Relation de l'Île Rodrigue*. In that document, an owl is described as one "which is very like the brown owl, and which eats little birds and small lizards. They almost always live in trees, and when they think the weather will be fine, they utter always the same cry at night." The Rodrigues Little Owl became extinct some time around 1730. The taxonomic identity of the second species from Rodrigues, Leguat's Owl (*Bubo leguati*), is not known with certainty. Described by Lord Rothschild, Leguat's Owl is known from a single tibiotarsus bone that is too large to be assigned to *Athene murivora*; in his book *Extinct and Vanishing Birds of the World*, J. C. Greenway remarked of Leguat's Owl that "it is now impossible even to assign it to a given genus". Regardless, Leguat's Owl was a distinct species, whether it belonged to *Bubo* or to another genus. Judging from the records of explorers to Rodrigues, Leguat's Owl probably disappeared from the island during the 1690's.

Also in the Indian Ocean, two strigids have become extinct on Mauritius: the Mauritius Scops-owl (*Otus commersoni*) and the

Mauritius Owl (*Strix sauzieri*). The latter is known only from bones, and the former from written descriptions of a large owl, nearly 60 cm in total length, with prominent ear-tufts and naked tarsi. Because of its large size, "*Otus commersoni*" may well have belonged to *Asio*; it was last reported in the forest of Mauritius in 1837.

Six of the 21 named subspecies of the Burrowing Owl are endemic to islands. Two that inhabited the West Indies, the race *guadeloupensis* of Guadeloupe and the race *amaura* of Antigua, became extinct around 1890. Both disappeared following the introduction of mongooses into the islands. The presence of man, either directly or indirectly, almost certainly brought about the demise of four species of *Grallistrix* that inhabited the Hawaiian Islands more than 1000 years ago (see Systematics), and several other taxa disappeared from islands in the Pacific and the Mediterranean after the arrival of humans. Without question, the number of strigid species driven to extinction following the colonization of islands by human beings is much larger than the above examples suggest.

In New Zealand, two races of the Laughing Owl, *albigacies* and *rufifacies*, inhabited South Island and North Island, respectively. The North Island race became extinct in about 1890. The decline of both subspecies coincided with increased numbers of ferrets, weasels and cats, which had been introduced to New Zealand to control rabbits. These predators undoubtedly found the owls and their nests to be easy prey. The South Island owls have not been observed since the 1950's, and many biologists have assumed that this race, too, is extinct. It is possible, albeit unlikely, that a few Laughing Owls exist in remote portions of the South Island's Southern Alps.

According to BirdLife International's 1994 appraisal of globally threatened birds, 21 (11%) of the 189 species of strigids known to be alive today are in danger of extinction, and another 14 (7.4%) are classified as Near-threatened. All but two of the threatened species live in the tropics, and many inhabit islands. BirdLife's classification scheme places threatened species into one of three categories, based on perceived risk of extinction. Critically Endangered species are at extremely high risk, with an estimated probability of extinction of 50% within five years. Endangered species face a 20% probability of extinction within 20 years, and Vulnerable species have an estimated probability of extinction of 10% within 100 years.

Four strigid species are considered Critically Endangered: these are the Seychelles Scops-owl, the Anjouan Scops-owl (*Otus capnodes*), the Comoro Scops-owl (*Otus pauliani*) and the Forest Owlet. The three scops-owls are endemic to islands in the Indian Ocean, where all are threatened by deforestation. The Seychelles Scops-owl occurs only in upland rainforest on the island of Mahé, the largest of the Seychelles; perhaps 80 pairs remain at 250-600 m elevation in an area threatened by the continued expansion of timber-collecting.

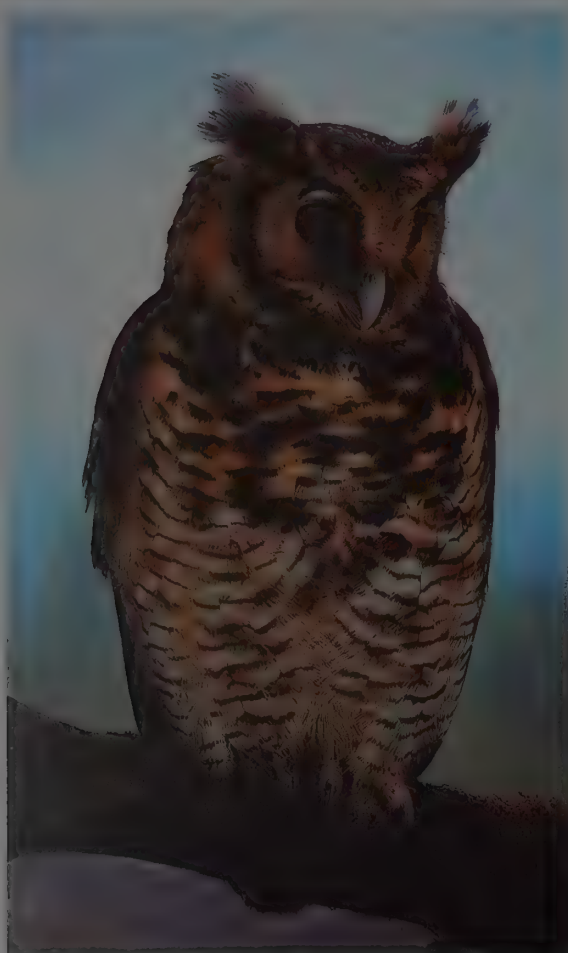
The Anjouan Scops-owl, which originally occurred on the islands of Anjouan (Ndzuani) and perhaps also Mayotte (Maore) in the Comoro Archipelago, was rediscovered in 1992 after not having been recorded for more than 100 years. Its initial disappearance was attributed to over-collecting by H. Humblot, who is suspected of having taken at least 33 specimens between 1884 and 1886. In 1993, R. J. Safford and associates estimated that 100-200 pairs were still present on Anjouan, in patches of upland forest above 800 m; unfortunately, more recent work indicates that only about 50 birds survive in a 10-km² block of forest that constitutes the last vestige of suitable habitat on Anjouan. Habitat loss is an obvious factor in the decline of this scops-owl, but it is also captured and eaten by people. Prospects for the species' survival are bleak, and it has been suggested that birds be translocated to nearby Moheli Island, which has been much less disturbed by humans and is the site of a proposed forest reserve; however, given the presence of the newly described Moheli Scops-owl on this small island (see Systematics), plans to introduce a second species of scops-owl would have to proceed with extreme caution, if at all.

Comoro Scops-owls are confined to wet, high-elevation forest on Grand Comoro (Ngazidja), which is the largest of the Comoro Islands. In late 1989, about 1000 pairs were estimated to inhabit 100 km² of suitable habitat existing on three sides of the island's highest peak, Mount Karthala. The forested parts of Grand Comoro are highly disturbed owing to widespread burning and logging, but trees that have colonized recent lava flows on Mount Karthala may provide habitat for the Comoro Scops-owl, and part of the mountain has been proposed as a forest preserve. In addition to habitat destruction, Comoro Scops-owls are considered to be vulnerable to competition for nesting cavities with introduced Common Mynas (*Acridotheres tristis*), which are increasing their range on the island.

Much attention has been focused in recent years on the plight of the Spotted Owl. This owl's requirement for old-growth and mature forest meant that a direct conflict arose between commercial interests and the aims of wildlife conservation. Despite management plans designed to assist the species' declining populations, the value of mature forest to the timber industry was so high that great pressure was put on politicians and land-managers to permit more cutting. After much discussion, scientists, politicians and commercial interests have failed to reach an agreement over the management of this owl's habitat, so that its future remains uncertain. The Mexican race, shown here, numbers no more than 1600 individuals, and is in a particularly perilous situation.



[*Strix occidentalis lucida*,
Arizona, USA.
Photo: John Cancalosi]



The rediscovery of the Forest Owlet more than 113 years after the last verified record is one of the most exciting ornithological events of the late twentieth century. During November 1997, P. C. Rasmussen, B. King and D. F. Abbott covered a 1200-km swath across central India in search of this elusive owl. Miraculously, they succeeded in locating a Forest Owlet in dry deciduous forest in the Tapti River Valley. The site was a new location for the species, and was 200 m higher in elevation than anywhere else where the bird had been encountered previously. The team returned the next day and found a second individual, and then relocated the original bird the day after that. In June 1998, Rasmussen revisited the region with a team of biologists from the Bombay Natural History Society. Team-members located a total of five Forest Owlets in two different areas in June and July, and they also obtained recordings of vocalizations and collected data on habitat characteristics and the species' behaviour. The owls occurred in densely forested valleys dominated by teak (*Tectona grandis*) trees. In the six months that had elapsed since Rasmussen's first visit, the area of forested habitat where the owls occurred had diminished drastically because of tree-cutting for cultivation. On the one hand, the rediscovery of the Forest Owlet, and the possibility that it occurs in other areas of similar habitat, is greatly encouraging. On the other hand, however, continued deforestation within the known range of the species is likely to be having a severe negative effect on the population, underscoring the need to survey the remaining habitat and to institute protective measures, if possible, wherever the owls are found.

Two of the four strigids classified as Endangered are from the Philippines: the Giant Scops-owl and the Philippine Eagle-owl (*Bubo philippensis*). Both species inhabit severely degraded rainforest on Mindanao, mainly in the lowlands, and the eagle-owl also occurs on Luzon, where it suffers from subsistence-hunting in addition to habitat degradation. Unfortunately, the same problem that besets these species, namely severe loss of habitat,

has also affected the Luzon Scops-owl (*Otus longicornis*), Mindoro Scops-owl (*Otus mindorensis*), Mindanao Scops-owl (*Otus mirus*) and Palawan Scops-owl, each of which is classified as Vulnerable. The first three species are probably not in immediate danger of extinction, because they inhabit montane forest that is typically the last to be cleared. However, the Palawan Scops-owl occurs in lowland forest, a habitat that is disappearing rapidly on the island, but it has also been found in mixed forest associated with cultivation. There are no population estimates available for these four scops-owls, but their numbers are almost certainly declining as the forested areas they inhabit continue to be destroyed and fragmented.

Blakiston's Eagle-owl is classified as Endangered. The Japanese declared it a "National Monument" in 1971, and the Ainu people of Hokkaido, northern Japan, called it "the god who defends the village", but despite such apparent reverence Blakiston's Eagle-owl has become a text-book example of a species that has declined at the hands of man. Only 300-400 pairs were estimated to occur in the Russian Far East in the mid-1980's, and about 80-100 birds, including 20 breeding pairs, were thought to reside on Hokkaido in 1991; Blakiston's Eagle-owl also occurred in north-eastern China, but may by now have been extirpated there. In 1998, T. Takenaka estimated that 30 breeding pairs and 120 individuals inhabited Hokkaido, with most of the birds occurring in the north-eastern corner of the island. Human encroachment, destruction of riparian forest, indiscriminate shooting, and depletion of fish populations are the major threats to the species. The situation is especially serious on Hokkaido, where most of the native forest has been converted to conifer plantations. Nearly 25% of the pairs on Hokkaido rely on an artificial feeding programme, and 40% of the breeding pairs nest exclusively in boxes. Although the small increase in population size between 1991 and 1998 may reflect the success of management efforts, recently documented cases of close inbreeding have been attributed to young birds returning to artificial feeding sites in their natal home range rather than dispersing naturally. Add to this the declining fish populations caused by dam construction and commercial fishing, and one is forced to conclude that the presence of humans continues to threaten the future of this magnificent species.

The Rufous Fishing-owl, the fourth Endangered strigid, is confined to the Upper Guinea forest and coastal mangroves in Guinea, Sierra Leone, Liberia, Ivory Coast and Ghana, and it has recently been found also in Nigeria. About 80% of the Upper Guinea forest is gone, and the remaining tracts are being felled so rapidly that most of the native forest outside protected reserves is expected to disappear within 20 years. To make matters worse, civil unrest in Liberia threatens the forest within Sapo National Park, so "protected" forest areas are in some cases vulnerable to disturbance as well. Nowhere common, the Rufous Fishing-owl is known from fewer than 30 records. It appears to be widespread only in Liberia and Sierra Leone, but even in these areas waste products from iron mines have severely polluted the rivers on which these owls depend for their food.

The three scops-owls that are classified as Vulnerable face the same combination of problems as the other threatened species: tropical deforestation and restricted geographical range. White-fronted Scops-owls inhabit lowland forest in South-east Asia and adjacent Indonesia. The extensive clearing of forest in this region is a well-known and serious problem, and it has imperilled a large number of bird species. Because they are lowland specialists, it will be difficult for White-fronted Scops-owls to maintain viable populations as habitat fragmentation continues. The Javan Scops-owl (*Otus angelinae*) is known from only two areas of montane forest in Java; it is quite secretive, and its exact status is unknown. The Sokoke Scops-owl (*Otus irenae*) is another lowland-forest specialist, until recently thought to be confined to the Arabuko-Sokoke Forest on the Kenyan coast, where a 1994 survey estimated that about 925 pairs occurred over an area of roughly 250 km². Since 1992, several Sokoke Scops-owls have been found in forest on the lower slopes of the East Usambara Mountains in north-eastern Tanzania, increasing hopes that larger numbers may occur there. Most of the world's Usambara Eagle-owls (*Bubo vosseleri*), numbering between 200 and 1000 individuals, inhabit evergreen forest at 200-1500 m elevation in the East Usambaras; a few indi-

The Usambara Eagle-owl is typical of a forest species with a restricted range that is threatened by habitat destruction. This owl, until fairly recently thought to be merely a subspecies of the more widespread Fraser's Eagle-owl (Bubo poensis), is found only in the Usambara and Uluguru Mountains of north-east Tanzania. As in so many parts of the world, development of the forest is the primary cause of concern. This species, a captive individual of which is shown here, is therefore considered Vulnerable.

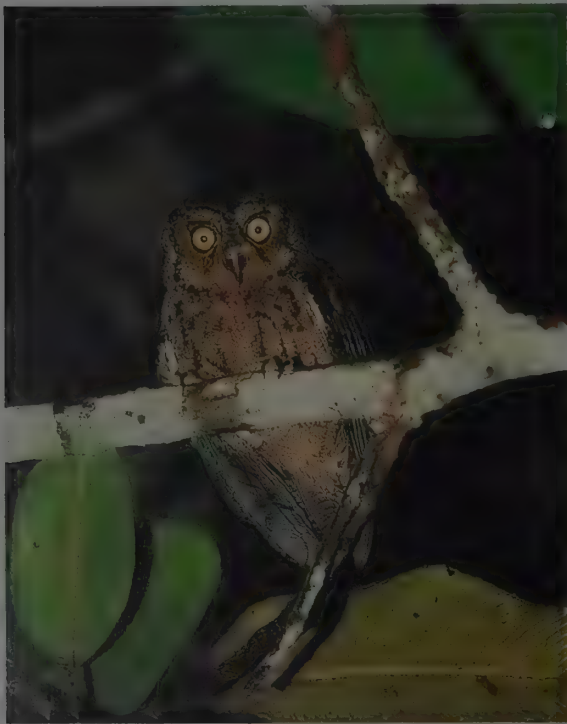
[*Bubo vosseleri*.
Photo: Eric &
David Hosking/FLPA]



Another species with a very restricted range in East Africa is the Sokoke Scops-owl. Until recently, this species was thought to be found nowhere outside the Arabuko-Sokoke Forest of coastal Kenya, a comparatively small area of approximately 372 km² in extent and holding a population of some 1000 pairs of these owls. With proper conservation and management of the forest, it would be possible to secure the survival of this and other species occurring in the region, but a long-term programme with this objective may have been jeopardized by withdrawal of financial support.

A glimmer of hope remains, however, since this scops-owl may be present also in the Kambai Forest Reserve in the East Usambaras of north-east Tanzania. In the latter region, two forest-conservation projects currently being undertaken should therefore assist not only the Usambara Eagle-owl (*Bubo vosseleri*), but also the Sokoke Scops-owl, both listed as Vulnerable by Birdlife International.

[*Otus ireneae*,
Arabuko-Sokoke Forest,
Kenya.
Photo: Luiz Claudio Marigo]



viduals of this Vulnerable species were recently discovered in the Uluguru Mountains south of the Usambaras, and a small number may also occur in the Nguru Mountains. Clearing of forest for subsistence-farming and tea plantations continues to be a problem in the region, and efforts to conserve lowland and montane forest in East Africa have been hampered by poor funding.

Apart from Blakiston's Eagle-owl, the Sichuan Wood-owl (*Strix davidi*) is the only other threatened strigid that occurs outside the tropics. Endemic to a small area in Qinghai and Sichuan provinces in China, it occupies areas of coniferous and mixed coniferous-deciduous forest at 2700-4200 m. This owl is considered by some authorities to be a subspecies of the widespread Ural Owl, but almost nothing is known of its biology. The main threat to the species is widespread deforestation, because its range is within one of the top timber-producing regions in China.

The mountains above the Albertine Rift Valley, along the borders of Zaire, Rwanda and Uganda, support another restricted-range species, the Albertine Owlet. Known from five records in scattered localities in the region, this rare and poorly known species is threatened by deforestation in the name of agriculture, timber production and gold-mining. The Albertine Owlet inhabits both montane and transitional forest. Although the transitional forest is accessible to farmers and thus in danger of clearing, hope exists for the species because the montane forest above the transitional zone is relatively intact. Political unrest in the area inhabited by this owl makes it difficult to predict the outcome of conservation measures.

The genus *Ninox* includes two species formally listed as Vulnerable and several other taxa that may warrant this designation. The Powerful Owl inhabits the band of eucalypt forest that stretches across south-eastern Australia from southern Queensland to Victoria. Although large numbers of individuals, perhaps as many as 10,000, occur in the area, much of the lowland forest frequented by this species has been cleared for agriculture. The Powerful Owl is especially vulnerable to loss of old-growth forest, a habitat that provides a high diversity of prey species and the large trees needed for nesting. The Sumba Boobook, endemic to the island of that name in the Lesser Sundas, is a poorly known species apparently confined to lowland rainforest and monsoon-forest. Significant amounts of forest have been cleared on Sumba to make way for cattle grazing and to provide firewood, and most of the forest that remains is highly fragmented.

The Christmas Hawk-owl is a *de facto* threatened species. Formerly considered a subspecies of the Moluccan Hawk-owl,

it is confined to the tiny 140-km² Christmas Island in the Indian Ocean. Despite its restricted range, it is fairly common, with an island-wide estimate of 560 pairs in 1997. Nonetheless, numbers must surely have declined since human settlement, owing to the clearing of 25% of the native forest for phosphate-mining earlier in the century. The Moluccan Hawk-owl complex contains several taxa that may prove to be valid species, including *hypogramma* from the Northern Moluccas, *hantu* from Buru, nominate *squamipila* from Seram, and *forbesi* from the Tanimbar Islands; each of these has a restricted range in Indonesia, and a taxonomic revision of the complex would probably result in important changes in the classification of the group, with significant implications for conservation. Likewise, the Philippine Hawk-owl may in fact constitute two species, one of which is probably threatened.

Until fairly recently, Hume's Owl was considered to be quite rare. Occurring only in Pakistan, southern Israel and the Sinai and Arabian Peninsulas, the species remained virtually unknown between 1878, when the type specimen was obtained in Pakistan, and the 1920's, when additional specimens were collected in the Judean Desert. One of several results of the oil boom in the Middle East was increased ornithological exploration of the region, and by 1975 Hume's Owl was known to be relatively common in Israel. Although this species has not been recorded in Pakistan since the first specimen was collected there in Makran, this region has not been well explored by ornithologists since the 1920's, so it is possible that small numbers still survive there.

The Fearful Owl occurs in primary and secondary rainforest at up to 500 m elevation on several of the larger islands in the Solomon chain. On the basis of BirdLife International's Endemic Bird Areas (EBA) scheme, more restricted-range species occur in the Solomons than in any other EBA. Much of the forest below 400 m has been commercially logged or cleared for coconut groves, and hunting is common on the islands. Very little is known about this owl's biology and population status, but, given its affinity for lowland forest, its numbers will almost certainly have declined during the twentieth century.

The philosophy behind BirdLife's Near-threatened designation arose from a need to highlight species that are close to being classified as threatened and for which considerably more information is needed in order to permit useful assessments. Six of the 14 Near-threatened strigids inhabit islands in the Old World, and each faces threats from deforestation: these are the Andaman Scops-owl, Sao Tome Scops-owl (*Otus hartlaubi*), Pemba Scops-owl, Wallace's Scops-owl (*Otus silvicola*), Chestnut-backed Owlet and Andaman Hawk-owl (*Ninox affinis*). In the New World tropics, so little is known about the Bearded and Colombian Screech-owls, the Unspotted Saw-whet Owl and the Buff-fronted Owl that the status of each is quite uncertain. Another two species, the Forest Eagle-owl and the Tawny Fish-owl, are fairly widespread in South-east Asia and adjacent China, but the montane forest they inhabit is fragmented and constantly threatened with destruction.

High-elevation cloudforest in the northern Andes of Peru supports the only known population of the Long-whiskered Owlet. This is a Near-threatened species because even small amounts of disturbance within its restricted range would be detrimental. Sadly, a recent survey in the Cordillera de Colán, one of only two localities known for the owl, revealed an "alarmingly high" rate of deforestation, with most of the forest having been cleared for marijuana and coffee plantations.

The Spotted Owl is the best-known strigid on the list of Near-threatened species, and it must certainly be the most abundant owl in this group. Realization in the 1970's that Spotted Owls in the Pacific North-west were confined to old-growth and mature forest, which is a scarce commodity in the region, led to a tremendous amount of research and management attention. Indeed, the species soon became the most-studied strigid in North America, if not the entire world. Concern for the owls on account of widespread loss of habitat and declining population sizes led to the designation of the northern (*caurina*) and Mexican (*lucida*) races as Threatened under the US Endangered Species Act in 1990 and 1993, respectively. The political, legal and economic ramifications of these listings had a profound influence

Three of the four Critically Endangered strigids are confined to islands in the Indian Ocean, where all are threatened by deforestation.

The Seychelles Scops-owl is found only on Mahé, the largest of the Seychelles group. It occurs at 250-600 m in the upland rainforest, where a population of no more than about 80 pairs is thought to survive. Even on this island, popular with tourists and frequently visited by scientists and conservationists, the forest habitat is under continued threat from the activities of timber-collectors.

[*Otus insularis*, Mahé, Seychelles. Photo: Eric & David Hosking/FLPA]



In eastern Asia, Blakiston's Eagle-owl offers a classic example of a species that has declined because of man's activities. This handsome and imposing owl was declared a "National Monument" in Japan in 1971, and was apparently revered by local tribespeople on Hokkaido, yet by 1991 its population on the latter island had plummeted to about 100 individuals, including 20 breeding pairs. A 1998 estimate put the Hokkaido population at 30 breeding pairs and 120 individual birds, mostly inhabiting the north-east of the island. Elsewhere, up to 400 pairs breed in south-east Russia, but the species is probably extinct in adjacent north-east China. This sorry situation has been brought about by destruction of native riparian forest, combined with human disturbance, persecution by hunters, and depletion of the fish stocks on which this owl lives. On Hokkaido, most of the natural forest has been replaced by conifers, and some 40% of the breeding pairs now nest solely in artificial boxes, while 25% of them are dependent on an artificial feeding programme. Moreover, immatures, rather than dispersing more widely, seem to return to feeding stations within their natal areas, leading to inbreeding among the small population. With fish stocks continuing to decrease as a result of commercial over-fishing and dam construction, the prospects for this Endangered owl, at least on Hokkaido, do not look good.

[*Bubo blakistoni*
blakistoni,
 Hokkaido, Japan.
 Photo: Steve Kaufman/
 DRK]



on wildlife management in the USA, and the Spotted Owl quickly became the hallmark species for conservation of old-growth forest in western North America.

The problem was, of course, that the commercial value of the mature forest required by the owls was extremely high, and the timber industry placed enormous pressure on land-managers and politicians to allow more cutting. By 1994, loss of old-growth habitat in the physiographic provinces of the Pacific North-west ranged from 54% to 99%. To make matters worse, unknown persons in some timber-dependent communities began shooting the owls, although mortality from this practice was thought to be low. In addition, recent range expansion by the closely related and more aggressive Barred Owl resulted in several cases of hybridization with Spotted Owls and may also have caused territory abandonment and direct mortality. Minimum estimates of population size, based on summaries by J. R. Gutiérrez and associates in 1995, gave about 3780 pairs and 1000 territorial individuals for the northern race, 3050 individuals for the Californian race *occidentalis*, and 800-1600 individuals for the Mexican race.

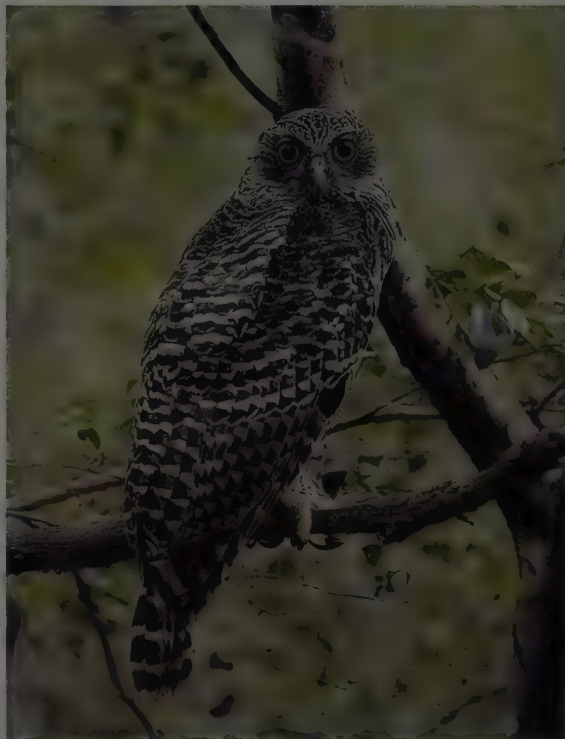
Three major conservation plans for Northern Spotted Owls were generated under the sponsorship of the US Government. The 1988 plan called for a series of 400-ha management areas in widely scattered localities in the Pacific North-west. The plan was soon abandoned, however, because it was deemed to have an unacceptably low probability of success. The second plan, put forth in 1990, recommended that large blocks of habitat on government-managed lands be set aside at intervals of 10-20 km. This plan was halted by litigation that forced the government to widen their conservation efforts to include all species associated with older forest in the region. A recovery plan as dictated by the Endangered Species Act was drafted in 1992, some 20 years after the owl was first known to be in trouble. This last effort was patterned after the 1990 plan, and included de-listing criteria and a formal recovery strategy. Largely for political reasons, however, the US Department of the Interior did not accept the plan, and no official recovery programme therefore exists for the species! Each of these plans has been criticized by scientists for being inadequate for the protection of viable populations of owls, while at the same time being distasteful to the timber industry,

which is already facing economic hardships independent of the Spotted Owl problem. As a result, scientists, politicians and commercial interests continue to disagree over the management of old-growth forest in general and Northern Spotted Owls in particular, and the situation is likely to remain unresolved for the near future.

Despite the plethora of negative factors stacked against it, the Spotted Owl's plight is not hopeless. The species will use intermediate-aged stands provided that key habitat elements, namely snags and large trees for nesting and cool micro-sites for roosting, are present, although the long-term reproductive success in these "second-class" habitats is unknown. Based on an increasingly large sample of marked individuals, research into demographics and other life-history aspects of the Spotted Owl will continue. Indeed, the population data gathered so far are among the best ever assembled for any owl, and, as knowledge of the species accumulates, the potential for solving some of its problems will increase as well.

As should be abundantly clear at this point, habitat loss is the greatest problem faced by strigids. The wide-scale degradation of forest habitat influences owls in several ways. First, many species rely on pre-existing tree cavities for nesting, and suitable sites are often limited even under natural conditions; thus, any reduction in the availability of cavity-bearing trees could have drastic effects on productivity. The problem can be especially acute for the larger species such as the Forest and Blakiston's Eagle-owls, Buffy Fish-owl, Pel's Fishing-owl, Spotted Owl and Powerful Owl, because the large trees they need for nesting are typically the first to go when a forest is exploited for saw timber. Second, severe fragmentation of forest interferes with the natural dispersal tendencies of owls and their prey species and reduces the amount of suitable habitat such that densities exceed carrying capacities; in this manner, fragmentation disrupts the functioning of entire communities, and organisms such as owls that are at the top of the food chain are often the most susceptible to the negative influences of these changes. Finally, some strigids simply cannot tolerate disturbance, in which case human encroachment can render an area unsuitable, even with relatively benign levels of habitat alteration.

By virtue of their predatory habits, raptors experience a suite of man-induced problems that seldom affect other groups of birds. For example, many owls are killed while pursuing prey, either being struck by automobiles or colliding with fences and



One of the least well-known of the world's strigids is the Javan Scops-owl. Indeed, this is believed to be the first colour photograph ever taken of this very rare species, which is listed as Vulnerable. It is known from only a couple of localities in western Java, where it inhabits montane forest. This owl appears to be unusually silent, making the task of monitoring it even more difficult. Its exact status is therefore uncertain, but the fact that forest areas throughout the world are fragile and threatened habitats is sufficient cause for concern over its conservation.

[*Otus angelinae*,
Gunung Gede Pangrango
National Park, Java.
Photo: Manuel Ruedi]

Although large numbers of Powerful Owls are estimated to live within the species' range in south-eastern Australia, this owl faces the same familiar problems as beset so many other strigids. Possibly as many as 10,000 individuals are thought to live in the eucalypt forest stretching from southern Queensland to Victoria, but here, as elsewhere, much of the lowland forest has already been cleared for agriculture. Loss of the nest-sites provided by old-growth forest, along with intensive forestry practices that reduce prey numbers, have made this once common species Vulnerable.

[*Ninox strenua*,
Australia.
Photo: Tom & Pam
Gardner/FLPA]

Found nowhere but on the volcano of Mount Karthala, the Comoro Scops-owl is considered Critically Endangered. It inhabits the highest forest areas, where available suitable habitat has been estimated at about 100 km². Although 1000 or more pairs could live within this area, the forest is suffering fragmentation through logging and fires. In addition, this owl has to face competition for nest-sites from the introduced Common Myna (*Acridotheres tristis*), which is spreading on the island. The Comoro Scops-owl is known only from the type specimen and a few photographs, the best of which is published here.

[*Otus pauliani*,
Mount Karthala,
Grand Comoro.
Photo: Alan Lewis]



powerlines. Larger owls such as *Bubo* and *Strix* are often electrocuted when they perch next to transformers and close-set powerlines. Collisions with and electrocutions by powerlines are thought to be especially important causes of mortality for Eurasian Eagle-owls in Sweden and Germany.

The killing of raptors in the belief that they are harming gamebird populations or preying on livestock continues to be a problem for hawks and eagles in some parts of North America, but the problem is probably not so great for owls. The situation appears to be different in Europe, however. Eurasian Eagle-owls were widely persecuted by gamekeepers and hunters during the first half of the twentieth century, and in some countries, particularly Italy, thousands of owls of several species were killed each year up to the mid-1970's. Tawny Owls are still shot or trapped near gamebird breeding pens in Britain. In eastern Russia, Blakiston's Eagle-owls are shot by hunters and fishermen during winter, when the owls are drawn to openings in the ice through which they catch fish. In many parts of China, owls are killed for medicinal purposes, despite having complete legal protection in the country, and unknown numbers of owls are shot in many developing countries, sometimes for food, sometimes out of sheer curiosity, and sometimes in the belief that they are bad omens or evil (see Relationship with Man). Owls are legally protected in most developed countries, however, and they do not seem to be the focus of systematic persecution anywhere, even in places where they continue to be shot or trapped. Moreover, it is important to keep in mind that direct mortality from the conscious acts of humans does not come close to matching the mortality that results from habitat destruction.

Pesticides pose another major threat. Use of the organochlorine DDT, in particular, had severe negative effects on breeding populations of Ospreys, Bald Eagles (*Haliaeetus leucocephalus*) and Peregrine Falcons (*Falco peregrinus*), primarily because the fish and birds on which these raptors fed had high levels of DDT residue in their tissues. Experimental studies of captive individuals suggested that owls were just as sensitive as diurnal raptors to the effects of DDT. Wild strigids largely escaped the problem, however, because the mammals and invertebrates that they consumed contained lower levels of toxins than did birds and fish.

Other pesticides have posed problems for owls on a local scale. Exposure to the anticholinesterase insecticide carbofuran

was associated with decreased reproductive success in Burrowing Owls in Canada. At various locations in the USA, carbofuran and another anticholinesterase, fenthion, caused direct mortality of Great Horned and Short-eared Owls, and mortality of Eastern Screech-owls and Great Horned Owls was attributed to organochlorines such as chlordane, dieldrin and endrin. The anticoagulant brodifacoum is used to control rodents, and a study in Virginia, USA, revealed the deaths of six Eastern Screech-owls and a Northern Long-eared Owl in fields where brodifacoum baits had been applied. In Minnesota, a Great Horned Owl and two Snowy Owls were killed after strychnine-treated grain was set out to kill Rock Doves; dove parts retrieved from the owl carcasses contained strychnine residues. The available evidence suggests that pesticides are currently not having major effects on strigid populations in North America, but the relative scarcity of studies makes it difficult to assess the extent of the problem.

The situation is much the same in Europe. Rodenticides, especially, have been linked with mortality in Barn Owls and also several strigids in Britain, and organic mercury compounds used as seed dressings caused considerable mortality of Eurasian Eagle-owls in Sweden prior to 1966. Declines in the numbers of Little Owls during the 1950's and 1960's in England and Belgium were attributed to pesticides, and, more recently, some individuals have shown evidence of PCB contamination. At present, however, evidence for widespread pesticide problems among owls seems to be absent in Europe.

Elsewhere in the world, the widespread use of insecticides has been cited as a potential problem for owls in China, but no data are available on actual contamination or mortality. Eurasian Scops-owls reportedly declined in northern Israel during the 1950's as a result of pesticide use, but the population appears now to be stable. Rodenticides have been implicated in population declines of Rufous and Barking Owls in Australia, and of Brown Fish-owls in Israel. In Kenya, a moribund Pearl-spotted Owlet was recovered one day after fenthion was applied to control a large communal roost of Red-billed Queleas (*Quelea quelea*); subsequent analysis for brain cholinesterase activity confirmed that fenthion was the cause of death.

Outside the tropics, populations of non-threatened strigids appear to be relatively stable in the New World, with the possi-



ble exception of the Burrowing Owl in North America. In response to widespread concern for the species, the First International Burrowing Owl Symposium was held in Seattle, Washington, in November 1992. The meeting attracted 130 participants from four countries, and papers were presented on a variety of topics that included population ecology and management. P. C. James and R. H. M. Espie reported the results of a survey in which they asked each wildlife agency in the 24 states and provinces within the species' range in the USA and Canada to estimate its population size and status. One state, Texas, reported a population estimate of more than 10,000 pairs, eleven states and provinces estimated 1000 to 10,000 pairs, and eight reported 100 to 1000 pairs; British Columbia, Manitoba, Minnesota and Iowa, however, reported fewer than 100 pairs. Despite these generally high numbers, 13 of the states and provinces believed that their populations were declining, and none reported an upward trend in numbers. Of the seven potential limiting factors identified, habitat loss was thought to be a major problem by 83% of respondents, rodent control and subsequent loss of nesting burrows by 54%, and pesticides by 46%. The first two factors are very likely to be real, because native grassland is fast disappearing from western North America, and the eradication of fossorial rodents, especially prairie-dogs, has been rampant. The survey revealed that hard data on Burrowing Owl population trends were scarce, despite the fact that the species is one of the world's easiest owls to observe and census. Quite appropriately, then, symposium participants identified the need to monitor population trends by means of long-term surveys as the top research priority for the species.

Interest in owl conservation is growing worldwide. The first international owl symposium, "Biology and Conservation of Northern Forest Owls", was held in Winnipeg, Manitoba, in 1987. The meeting was a huge success and was followed, ten years later nearly to the day, by the second international symposium in Winnipeg, "Biology and Conservation of Owls of the Northern Hemisphere". The inclusion of non-forest owls in this symposium reflected the increased awareness of the potential problems of all Northern Hemisphere species. The third international owl symposium will be held in Canberra, Australia, in 2000, and will be unlimited as to species and geographical coverage. Also active on a global scale is the World Working Group on Birds of Prey and Owls, which began with a focus on diurnal raptors nearly 30 years ago and has held five world conferences since its inception. The group's third conference, held in Eilat, Israel,

was noteworthy in being the first one at which the group devoted a major session to owls.

Despite the growing interest in owls, conservation efforts on their behalf have lagged behind those for falconiforms, in part because of the relative lack of pesticide problems, but also because there was no active support group for the Strigidae such as that which existed for hawks, eagles and falcons, namely falconers. The husbandry that developed through the ancient art of falconry led to practices, such as captive propagation and reintroduction, that proved to be useful techniques in the modern world. Many strigid species are held in zoos, but breeding programmes devoted to releasing owls into the wild are relatively scarce compared with those for falconiforms. Captive breeding has been successful in re-establishing Eurasian Eagle-owls in Germany and Sweden, where their populations were severely diminished in the first half of the twentieth century. Similarly, Eurasian Pygmy-owls, extirpated from Germany's Black Forest after World War II, are now flourishing in that region owing to the release of 35 captive-bred individuals between 1968 and 1971; the population currently stands at more than 150 breeding pairs. Reintroduction of captive-bred Ural Owls into the Bavarian National Park in Germany has not been quite so successful as the eagle-owl and pygmy-owl work, but five released birds became established in the wild between 1972 and 1986. The Peregrine Fund's World Center for Birds of Prey in Boise, Idaho, is one of the world leaders in captive propagation of threatened raptors. Although the Peregrine Fund has not yet bred owls in captivity, it has provided direct support for research on Mottled and Black-and-white Owls in Guatemala (the Maya Project) and on Sokoke Scops-owls in Kenya.

The most active captive-release programme in North America is for Burrowing Owls, where reintroductions have been attempted in Manitoba, British Columbia and Minnesota and have been proposed for other areas. In addition, active nests of this species that were threatened by development have been successfully moved to artificial burrows, and the owls can also be induced to settle in areas where artificial burrows have been provided in the absence of natural sites. Such willingness to accept artificial nesting structures holds much promise for the conservation of the Burrowing Owl as numbers of fossorial rodents continue to decline in western North America.

An alternative to captive-breeding was used to bolster numbers of a Critically Endangered subspecies of *Ninox* on a Pacific island. Two male Moreporks (*Ninox novaeseelandiae*) of the nomi-



A comparatively large percentage of the world's owls are poorly known, a fact which, in itself, renders their conservation status uncertain.

The Tawny-browed Owl of eastern South America is just one example.

This species inhabits tropical rainforest and open woodland, where it is considered at best uncommon. Little is known about its biology and ecology. It appears to have declined in parts of its range, with timber-cutting a probable cause, and the scale of habitat loss in other parts is thought such that monitoring of its populations is strongly advised.

[*Pulsatrix koenigswaldiana*, Itatiaia National Park, Brazil.

Photo: Joe Tobias]

Another of the world's rare and poorly known strigids is the Fearful Owl of Bougainville and two of the islands in the Solomons. This owl lives in lowland primary forest and tall secondary forest and is reported to feed on phalangers (Phalanger), which occur in large numbers on Santa Isabel and are eaten also by local people. Forest destruction, however, seems to be the main threat facing this owl, which is listed as Vulnerable.

[*Nesasio solomonensis*, Santa Isabel, Solomon Islands.

Photo: Guy Dutson]

One of the encouraging stories of the last decade of the twentieth century has been the rediscovery of the Forest Owlet. First found in 1872, the species was recorded a few times in the 1880's, but there were no further confirmed records until November 1997, when two individuals were located in dry deciduous forest in the Nandurbar district of Maharashtra, India. In June 1998, a team of scientists set out to determine the species' exact status, with detailed surveys, vegetation sampling, searching for pellets, and behavioural observations on the two individuals already found. Tape recordings of these were also made. The results should enable this rare owl's current status to be properly assessed.

[*Athene blewitti*,
Maharashtra, India.
Photo: Farah Ishtiaq]



nate race were released on Norfolk Island in 1987 in an attempt to provide a mate for a lone female of the race *undulata*, the Norfolk Boobook, which was believed to be the sole survivor of that race of the Morepork. Nestboxes were set out and protected from rats, and the owls were carefully monitored so as to avoid disturbance. The resident female paired with one of the males almost immediately; their first nesting attempt, in 1988, failed, but the pair succeeded in raising two chicks in each of the years 1989 and 1990. In establishing what essentially will become a population of hybrids, conservationists hope to preserve gene complexes that are adapted to life on this tiny Pacific outpost.

Artificial nests, usually in the form of nestboxes or walled platforms, have been used with great success for many species, including the Flammulated Owl, several screech-owls, Blakiston's Eagle-owl, Tawny, Ural and Great Grey Owls, Northern Hawk-owl, several pygmy-owls, and Little and Boreal Owls (see Breeding). In Britain, Northern Long-eared Owls readily take to wooden baskets placed in trees. Nestboxes are great tools that allow researchers access to owls, which can then be marked and recaptured. They also have high potential for management in areas where natural cavity nests are scarce owing to timber harvest. It is, however, important to keep in mind that management efforts should not rely on nestboxes as an alternative to implementing sound forestry practices that allow for the retention of natural nest-sites.

Although a rather dismal picture appears to have been painted for the status of many strigids, all is not gloom and doom. Many owls co-exist quite well with humans. This is illustrated by the Eurasian Scops-owl, Tawny Owl and Little Owl in Europe; the Oriental and Pallid Scops-owls and Brown Hawk-owl in Asia; the Northern White-faced Owl, Spotted Eagle-owl and Pearl-spotted Owlet in Africa; the Southern Boobook in Australia; the Morepork in New Zealand; the Ferruginous Pygmy-owl in Central and South America; and the Eastern Screech-owl, Great Horned Owl and Burrowing Owl in North America. Indeed, habitat alterations have benefited some species, especially those that hunt in more open areas. Examples include Burrowing Owls that have moved into cleared areas in South America, Northern Long-eared and Short-eared Owls that hunt in pastures that support large numbers of voles, and Snowy Owls that move south in

winter to settle in cultivated areas and open spaces adjacent to airport runways.

As is true for the conservation of any group of organisms, the future wellbeing of the Strigidae will depend in part on the success of biologists and conservationists in convincing others of the value of biodiversity, and in finding creative ways to provide people with the incentive to conserve their natural resources.

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PLATE 4

inches 4
cm 10



1



2



ssp icterorhynchus



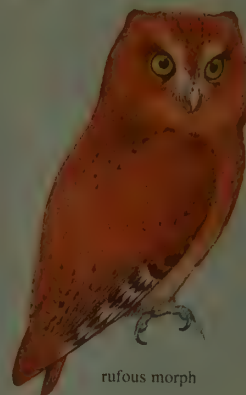
grey-brown morph

4



ssp holerythrus

3



rufous morph



grey-brown morph

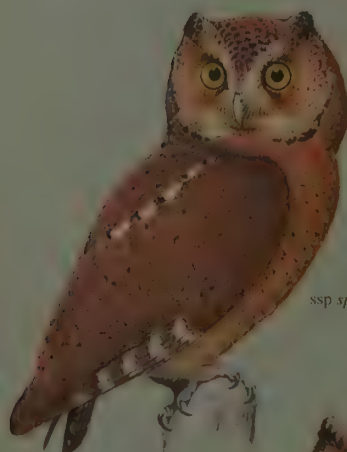
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rufous morph



6

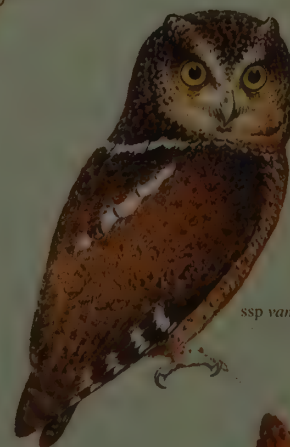


ssp spilocephalus



ssp luciae

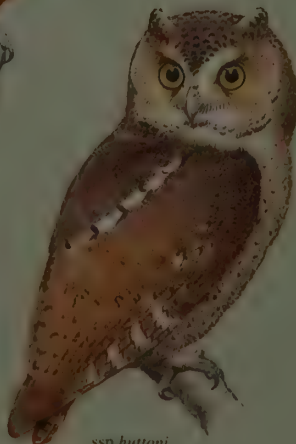
7



ssp vandewateri



ssp hambroeki



ssp huttoni



form "stresemanni"

Subfamily STRIGINAE

Tribe OTINI

Genus *OTUS* Pennant, 1769

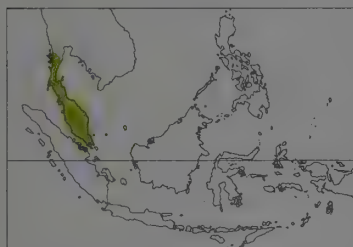
1. White-fronted Scops-owl

Otus sagittatus

French: Petit-duc à front blanc **German:** Weißstirneule **Spanish:** Autillo Frentiblanco
Other common names: Greater/Large/Malayan Scops-owl

Taxonomy. *Ephialtes sagittatus* Cassin, 1848, Malacca.
Relationships unclear. Monotypic.

Distribution. S Myanmar (Tenasserim), S Thailand and Malay Peninsula; possibly Sumatra (status uncertain).



Descriptive notes. 25-28 cm; c. 120 g. Along with *O. megalotis*, the largest Old World *Otus*. Forehead, eyebrows, lower part of long ear-tufts and lower part of face prominently whitish; upperparts intense chestnut or rufous-brown with obscure buff spots, scapulars edged paler; tail and wings barred; underparts light cinnamon-rufous, with chestnut across upper breast, and with black arrow-shaped markings; eyes brown (sometimes yellow?); bill and feet bluish-white; tarsus feathered. Distinguished from other *Otus* by large size, longer tail and pale face markings. Sexes apparently alike. Juvenile undescribed. Voice. A hollow, whistled

"hooo" very like that of *O. rufescens*, but with more abrupt start and finish; low soft moans also described.

Habitat. Primary tropical forest, especially lowland evergreen forest in Thailand and Malaysia; also tall secondary forest and rather degraded swampy forest. Mainly a lowland specialist, but recorded in foothills to c. 700 m.

Food and Feeding. No information.

Breeding. Lays Feb-Mar; nest in tree hole; 3-4 eggs. No other information.

Movements. Resident in Thailand and, presumably, elsewhere.

Status and Conservation. VULNERABLE. CITES II. Described as rare or very rare and declining throughout its range, but very poorly known; may prove locally more common in Malaysia, e.g. at Pasoh Forest Reserve shown by long-term mist-netting to be no less common than other scops-owls, but surprisingly few recent records. In Thailand, recent reported sightings in W Central Plains, well N of previous known range, included 3 roosting together, perhaps indicative of wider distribution than realized. Only 1 record from Sumatra, of undated specimen in Aceh; perhaps only vagrant there. Although has been considered an extreme lowland-forest specialist, has been recorded in foothills and is able to tolerate rather degraded forest with swampy patches. Extensive lowland deforestation considered greatest threat to survival.

Bibliography. Andrew (1992), Collar & Andrew (1988), Collar *et al.* (1994), Delacour (1947), Glenister (1951), Holmes (1996), Lekagul & Round (1991), MacKinnon & Philipps (1993), van Marle & Voous (1988), Marshall (1978), Medway & Wells (1976), Riley (1938), Robson (1998), Round (1988), Smythies (1986), Wells (1999), Zhao Zhengjie (1995).

2. Reddish Scops-owl

Otus rufescens

French: Petit-duc roussâtre **German:** Rötteleule **Spanish:** Autillo Rojizo
Other common names: Rufescent/Rufous Scops-owl

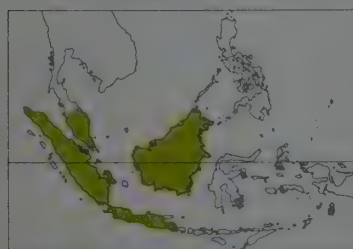
Taxonomy. *Strix rufescens* Horsfield, 1821, Java.

Relationships unclear. Additional race *burbridgei* based on single dark-faced specimen from Sulu Is, in Philippines, but record apparently not accepted as origin of specimen disputed; description also thought possibly not outside normal variation of nominate race. Two subspecies recognized.

Subspecies and Distribution.

O. r. malayensis Hachisuka, 1934 - S peninsular Thailand and peninsular Malaysia.

O. r. rufescens (Horsfield, 1821) - Sumatra, Bangka, Java and Borneo.



Descriptive notes. 15-18 cm; c. 77 g. Forehead, conspicuous ear-tufts, eyebrows and chin pale buffy to white; upperparts tawny-rufous with small light to buff spots, particularly on scapulars, where often triangular or arrowhead-shaped; underparts paler, more cinnamon, with dark spots; iris brown or yellowish-gold; bill generally flesh-coloured to horn; feet flesh-coloured or yellowish. Differs from *O. sagittatus* in much smaller size. Juvenile similar, but less spotted. Race *malayensis* slightly more rufous above and more rufous-ochre below than nominate. Voice. A hollow whistle, "hoooo", repeated at intervals of c. 7-11 seconds.

Habitat. Lowland to submontane forest in Borneo; lowland rainforest or peat-swamp forest in Thailand and Malaysia; in Sumatra, occurs also in tall secondary forest, apparently including logged areas. Primarily a specialist of primary rainforest below c. 1000 m, mainly up to 600 m.

Food and Feeding. No information.

Breeding. Lays Mar-Apr; nestling found in Jul in Java. Nest in natural tree hole or old hole of woodpecker or barbet. Chick with reddish-brown down.

Movements. Resident; possibly some altitudinal movement locally.

Status and Conservation. Not globally threatened. CITES II. Rare throughout range, and probably declining in most parts, but elusive and little known. In S Malay Peninsula said to be regular and uncommon to more or less common, but in S peninsular Thailand known only from recently discovered population in Chalerm Prakit Wildlife Sanctuary and from Nakhon Si Thammarat. Considered threatened by habitat destruction in Thailand. Occurs in a series of protected areas throughout its range, such as Taman Negara National Park and Panti Forest Reserve in Peninsular Malaysia, Way Kambas National Park in Sumatra, and Danum Valley Conservation Area and Gunung Mulu National Park in Borneo.

Bibliography. Andrew (1992), Delacour (1947), Delacour & Mayr (1946), Glenister (1951), Holmes (1996), Holmes & Burton (1987), Lekagul & Round (1991), MacKinnon (1988), MacKinnon & Philipps (1993), van Marle & Voous (1988), Marshall (1978), Medway & Wells (1976), Nash, S.V. & Nash (1985, 1988), Round (1988), Smythies (1981), Wells (1999).

3. Sandy Scops-owl

Otus icterorhynchus

French: Petit-duc à bec jaune **German:** Gelbschnabeule **Spanish:** Autillo Piquigualdo
Other common names: Cinnamon Scops-owl

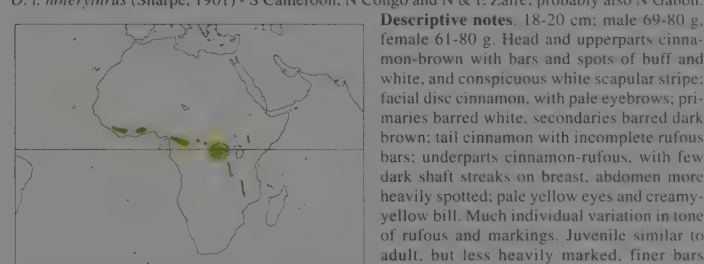
Taxonomy. *Scops icterorhynchus* Shelley, 1873, Fantee, Ghana.

Probably forms superspecies with *O. irenae*. Has been considered conspecific with Asian *O. balli* on basis of morphology, but differs significantly in plumage and vocal characters. Some authors have included Sumatran form "*stresemanni*" of *O. spilocephalus* as race of present species, or with the two forming a superspecies. Two subspecies recognized.

Subspecies and Distribution.

O. i. icterorhynchus (Shelley, 1873) - Liberia, Ivory Coast and Ghana.

O. i. holerythrus (Sharpe, 1901) - S Cameroon, N Congo and N & E Zaire; probably also N Gabon.



Descriptive notes. 18-20 cm; male 69-80 g, female 61-80 g. Head and upperparts cinnamon-brown with bars and spots of buff and white, and conspicuous white scapular stripe; facial disc cinnamon, with pale eyebrows; primaries barred white, secondaries barred dark brown; tail cinnamon with incomplete rufous bars; underparts cinnamon-rufous, with few dark shaft streaks on breast, abdomen more heavily spotted; pale yellow eyes and creamy-yellow bill. Much individual variation in tone of rufous and markings. Juvenile similar to adult, but less heavily marked, finer bars above and less streaked below. Race *holerythrus* more rufous, with less breast streaking. Voice. A drawn-out whistle, "twoooo", up to 1 second long, dropping in pitch and volume, given at intervals of 3-4 seconds. May respond to call of *Bubo poensis*.

Habitat. Lowland evergreen forest; in Liberia, recorded in high forest, including logged areas, and also in forest-shrub-grassland mosaic; in N Congo, recently reported from open-canopy forest. From sea-level to 1000 m.

Food and Feeding. Stomach contents of collected specimens included crickets and grasshoppers. Captive bird consumed only insects, taken at dawn and dusk but not during night.

Breeding. Detailed information unknown. Possibly lays Feb-Mar; nestling found in Zaire in May and juveniles in Cameroon in Apr; in Liberia (Mt Nimba), 2 males in Jun/Jul had small gonads, and female in Sept had enlarging ovaries.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Appears to be rare throughout its fragmented range; only 4 known specimens, 2 from each of Ghana and Cameroon. Assessment of status difficult, owing to its poorly documented distribution and biology. In Liberia, found to be present in all forest areas where intensive study has taken place, and thought to be probably not uncommon.

Bibliography. Bannerman (1953), Bowden & Andrews (1994), Christy & Clarke (1994), Colston & Curry-Lindahl (1986), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Dowsett *et al.* (1999), Dowsett-Lemaire & Dowsett (1998a), Fry *et al.* (1988), Gatter (1988, 1997), Grimes (1987), Kemp & Kemp (1998), Lippens & Wille (1976), Louette (1981), Mackworth-Præd & Grant (1970), Marshall (1978), Snow (1978), Stephenson & Newby (1997), Thiollay (1985).

4. Sokoke Scops-owl

Otus irenae

French: Petit-duc d'Irène **German:** Sokokeeule **Spanish:** Autillo de Sokoke
Other common names: Morden's Scops-owl

Taxonomy. *Otus irenae* Ripley, 1966, Sokoke-Arabuku Forest, Kenya.

Probably forms superspecies with *O. icterorhynchus*. Monotypic.

Distribution. Sokoke-Arabuku Forest in SE Kenya, and NE Tanzania (lowlands N of E Usambara Mts).

Descriptive notes. c. 15-18 cm; 45-50 g. Occurs in dark brown, grey-brown and rufous morphs. Crown streaked dusky brown, small ear-tufts generally not visible in the field; nape feathers have pale bases, giving spotted effect; facial disc light rufous to brown and buff, with whitish or buffy eyebrows; wing-coverts finely vermiculated; flight-feathers barred whitish-cream and brown; tail with incomplete dark brown and pale bars; underparts paler than upperparts, with darker wash on chest, and few sooty spots; cere and eyes yellow; bill horn-coloured to blackish. Juvenile very like adult. Voice. A whistled "too-too-too..." given in series of 5-10 notes, and repeated c. 10 times per minute; calls most frequently 2 hours before dawn and 2 hours after dusk.

Habitat. Forest. Generally prefers *Cynometra-Brachylaena* forest on red magarini sands, but also occurs in *Cynometra* thicket, and in *Azelia-Cynometra* forest on white soils; occasionally wanders



into *Brachystegia* woodland; absent where canopy below 3-4 m. Lowlands up to 70 m, but found at 200-400 m in E Usambaras.

Food and Feeding. Mainly insects; stomach contents from a few individuals showed arboreal leaf-eating insects such as crickets, katydids and phasmids. Some crepuscular activity, but mostly nocturnal. May use perch for hunting, dropping on to prey; in most observations, seen perched 3-4 m above ground.

Breeding. Breeding habits unknown.

Movements. Unknown, but probably largely sedentary owing to its restricted range. Evidence of some dispersal away from normal habitat.

Status and Conservation. VULNERABLE. CITES I. Restricted-range species; present in Tanzania-Malawi Mountains EBA and East African Coastal Forests EBA. Kenyan population estimated at c. 1000 pairs in 1984, and about the same in 1994, with density of 7-8 pairs/km² in preferred habitat; considered locally common. Further study on distribution needed; may occur N of Sokoike in the Mundane Range, where suitable habitat exists; thought possibly more widespread and more numerous in N Tanzania, following records in Kambai and Kwangumi Forest Reserves. Forest destruction the major threat. Although Sokoike Forest Reserve (400 km²) provides limited forest protection, commercial logging of *Brachylaena* trees for the carving industry and other valuable timber occurs; 43 km² nature reserve established inside the forest reserve by the Kenyan Ministry of Natural Resources and, although no cutting permitted, instances of large-scale felling still reported; conservation regulations ignored perhaps because of lack of funds for enforcement. Also, areas of forest outside the reserve being cleared for exotic plantations. Proposed conservation measures include increasing size of nature reserve to 60 km², and setting aside 200 km² of surrounding forest reserve for traditional uses only; also, improving facilities for forest officers to enable them to carry out and enforce policies. Conservation efforts impeded by lack of funding.

Bibliography. Alexander (1995), Bennun & Njoroge (1996), Britton (1976, 1980), Britton & Zimmerman (1979), Britton *et al.* (1984), Brown (1977), Clark & Mikkola (1989), Collar & Andrew (1988), Collar & Stuart (1985, 1988b), Collar *et al.* (1994), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Evans, T.D. (1997), Evans, T.D., Hague *et al.* (1994), Evans, T.D., Tye *et al.* (1997), Evans, T.D., Watson *et al.* (1994), Fanshawe (1993, 1994), Fry *et al.* (1988), Hipkiss *et al.* (1994), Kelsey & Langton (1984), Kemp & Kemp (1998), King (1978/79), Knox & Walters (1994), Lewis & Pomeroy (1989), Marshall (1978), Ripley (1966), Ripley & Bond (1971), Short *et al.* (1990), Shuker (1993), Snow (1978), Stattersfield *et al.* (1998), Zimmerman, D.A. *et al.* (1996).

5. Andaman Scops-owl

Otus balli

French: Petit-duc des Andaman German: Andamaneule Spanish: Autillo de Andamán

Taxonomy. *Ephialtes Balli* Hume, 1873, South Andaman Island.

Probably forms superspecies with *O. alfredi* and *O. spilocephalus*. Has been considered conspecific with African *O. ieterorhynchus* on basis of morphology, but significant differences in plumage and vocal characters indicate that the two are better treated as separate species. Some authors have included Sumatran form "*stresemanni*" of *O. spilocephalus* as race of present species, or with the two forming a superspecies. Monotypic.

Distribution. Andaman Is.



Descriptive notes. 18-19 cm. Occurs in rufous and grey-brown morphs, former less variegated. Fairly prominent ear-tufts and pale eyebrows; upperparts sparsely peppered with black and whitish spots, numerous white spots on crown and neck can to some extent resemble a collar; flight-feathers barred white, brown and tan, tail barred brown and tan; underparts much paler and greyer than upperparts, chest finely vermiculated, with thin black spots throughout; iris yellow, hazel or brown; bill yellow or greenish-horn; tarsus bare for third to half its length; feet flesh-grey to greenish-yellow. Differs from *O. spilocephalus* in

rougher plumage texture, relatively more conspicuous black and white flecking over plumage and lack of pale scapular stripe. Juvenile not described. Voice. A strong, loud "hoot! hoot-curroo", with characteristically rolled "r".

Habitat. Trees in semi-open areas, settlements and cultivated areas; gardens; has been known to enter bungalows.

Food and Feeding. Primarily caterpillars, also beetles and other insects. Captures caterpillars from foliage by sidling up to them in a parrot-like fashion. Strictly nocturnal.

Breeding. Lays Feb-Apr. Nest in natural tree hollow or in abandoned hole of woodpecker or barbet, usually 2-4 m above ground, 2-3 eggs.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Andaman Islands EBA. Currently considered Near-threatened. Considered quite common, or at least readily located. Appears to accept presence of human beings, and associated with agriculture; despite this, forested habitat in Andamans is decreasing rapidly, and this could represent a threat in the long term.

Bibliography. Ali & Ripley (1981), Butler (1899), Grimmett *et al.* (1998), Inskipp *et al.* (1996), Marshall (1978), Ripley (1982), Stattersfield *et al.* (1998), Tikader (1984).

6. Flores Scops-owl

Otus alfredi

French: Petit-duc de Florès German: Floreseule Spanish: Autillo de Flores
Other common names: Everett's Owl/Scops-owl, Flores Spotted Scops-owl

Taxonomy. *Pisorhina alfredi* Hartert, 1897, Repok Mountains, above 3500 feet [c. 1100 m], Flores. Probably forms superspecies with *O. balli* and *O. spilocephalus*. Recently treated as a rufous morph of race *albiventris* of *O. magicus*, but morphological study clearly demonstrates its distinctness and validity as a species. Monotypic.

Distribution. Flores I, in Lesser Sundas.



Descriptive notes. 19 cm. Facial disc solid dark rufous-brown, with white eyebrows and rufous ear-tufts; forehead with fine white markings, crown unstreaked rufous; upperparts uniform dark rufous with no barring or streaking, but instead a hindneck-collar of small white triangles; outer webs of scapulars white with large brown spangles; flight-feathers barred rufous and white; tail essentially unbarred; underside white, chest occasionally tinted rusty-brown, with faint, fine dark vermiculation and rufous barring; bill and iris yellow; feet and claws yellow, the latter without dark tips; feet proportionately smaller than

in other *Otus*, and tarsi thickly feathered except for the bare distal quarter. Juvenile almost uniformly pale rufous with a little faint barring; tail bands more evident. VOICE. No information; believed possibly largely silent.

Habitat. Mountain forest above 1000 m.

Food and Feeding. No information.

Breeding. No information.

Movements. No information. Presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Northern Nusa Tenggara EBA. The little information known about this species is from original notes on the first 3 specimens, collected late in 19th century; no new specimens until one collected in May 1995 on Poco Mandasawu, and another netted and photographed in Mar 1995 in Danau Rana Mese, a crater lake within Ruteng Recreation Park, but not correctly identified until 1998. Single brief sighting in 1997, in forest near Danau Rana Mese. True status unknown, but almost certainly rare; probably not listed as threatened because true specific status misunderstood. That species occurs in a recreation park provides optimism for establishment of a protected area there.

Bibliography. Andrew (1992), Coates & Bishop (1997), Collar & Andrew (1988), Inskipp *et al.* (1996), Jepson & Monk (1995), Marshall (1978), Monk *et al.* (1997), Pilgrim & Leadley (1995), Rasmussen (1998b), Stattersfield *et al.* (1998), Sujatnika *et al.* (1995), White & Bruce (1986).

7. Mountain Scops-owl

Otus spilocephalus

French: Petit-duc tacheté German: Fuchseule Spanish: Autillo Montano
Other common names: Spotted/Spotted Mountain Scops-owl; Bornean Scops-owl (*luciae*); Vandewateri's Scops-owl (*vandewateri*); Stresemann's (Mountain) Scops-owl ("*stresemanni*")

Taxonomy. *Ephialtes spilocephalus* Blyth, 1846, Darjeeling.

Probably forms superspecies with *O. balli* and *O. alfredi*. Previously considered by some to include *O. angelinae* and *O. longicornis* as races, but differences in vocalizations indicate that all are separate species. Race *vandewateri* sometimes treated as full species, and sometimes as race of *O. angelinae*, but morphology and voice suggest better regarded as race of present species. Mt Kerinci (Sumatra) foothills form "*stresemanni*" variously regarded as race of present species, of *O. ieterorhynchus* or of *O. balli*, or even as full species forming superspecies with either of last 2; known only from single specimen collected in 1914, but has not been relocated and its status is uncertain; although has been suggested as pale form of *vandewateri*, this not borne out by comparison of the few available museum specimens. Current racial divisions and geographical limits obscure; populations in Bangladesh, Nagaland and Manipur sometimes separated as race *rupchandi*. Eight subspecies recognized.

Subspecies and Distribution.

O. s. huttoni (Hume, 1870) - N Pakistan E to C Nepal.

O. s. spilocephalus (Blyth, 1846) - C Nepal E to Arunachal Pradesh and Myanmar.

O. s. latouchi (Rickett, 1900) - N Thailand and Laos to SE China and Hainan.

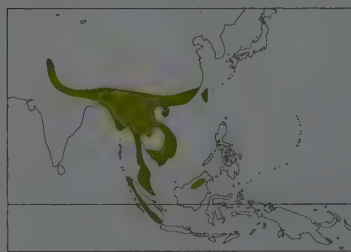
O. s. hambroeki (Swinhoe, 1870) - Taiwan.

O. s. siamensis Robinson & Kloss, 1922 - S Thailand to S Vietnam.

O. s. vulpes (Ogilvie-Grant, 1906) - Malay Peninsula.

O. s. vandewateri (Robinson & Kloss, 1916) - Sumatra.

O. s. luciae (Sharpe, 1888) - Borneo.



Descriptive notes. 17-21cm; c. 55-120 g. Plumage highly variable; some races polymorphic. Nominate race with facial disc whitish to light rufous with light brown bars, whitish eyebrows; upperparts rufous-brown, varying from russet to dusky brown, vermiculated darker, with crown and relatively small ear-tufts black-spotted; sometimes hint of pale hindneck-collar; scapulars with black tipped silver-white spots; flight-feathers and tail barred; underparts finely vermiculated rufous and buff, with paired small black and white spots; tarsus completely feathered; iris yellow and bill creamy. Juvenile duller, more barred.

Races differ mainly in plumage coloration: *huttoni* much paler, lacking rufous morph, grey-brown above, whitish with black spots below; *latouchi* more strongly rufous; *hambroeki* with no rufous morph, dark brown above, prominent pale collar, buffish and finely streaked below, with very distinct pale facial disc and long bicoloured ear-tufts; *siamensis* dark; *vulpes* dark rufous with black markings above; *luciae* heavily marked and dark overall, no collar, rufous-brown to buff-brown with black bars above, well vermiculated below; *vandewateri* very dark brown to rufescent with prominent pale collar, blotchy dark markings above, finer scrawls below on rufescent or brown background; "*stresemanni*" rich rufous with white forehead and fine white speckles overall, no collar. VOICE. Very vocal. Clear, piercing, two-note whistle, "plew-plew" or "he-he", repeated every 5-10 seconds.

Habitat. Dense evergreen forest, especially with chestnut, oak and rhododendron, sometimes with pine; also montane forest, gullies and ravines; locally, exploits dense regrowth at forest edge. From foothills to 2600 m, occasionally to 2750 m.

Food and Feeding. Primarily moths, beetles, mantises, cicadas and other insects; also takes small rodents and birds, and perhaps lizards. Hunts mainly beneath canopy, in lower strata of dense vegetation; reported to keep close to ground. Strictly nocturnal; rarely seen by day.

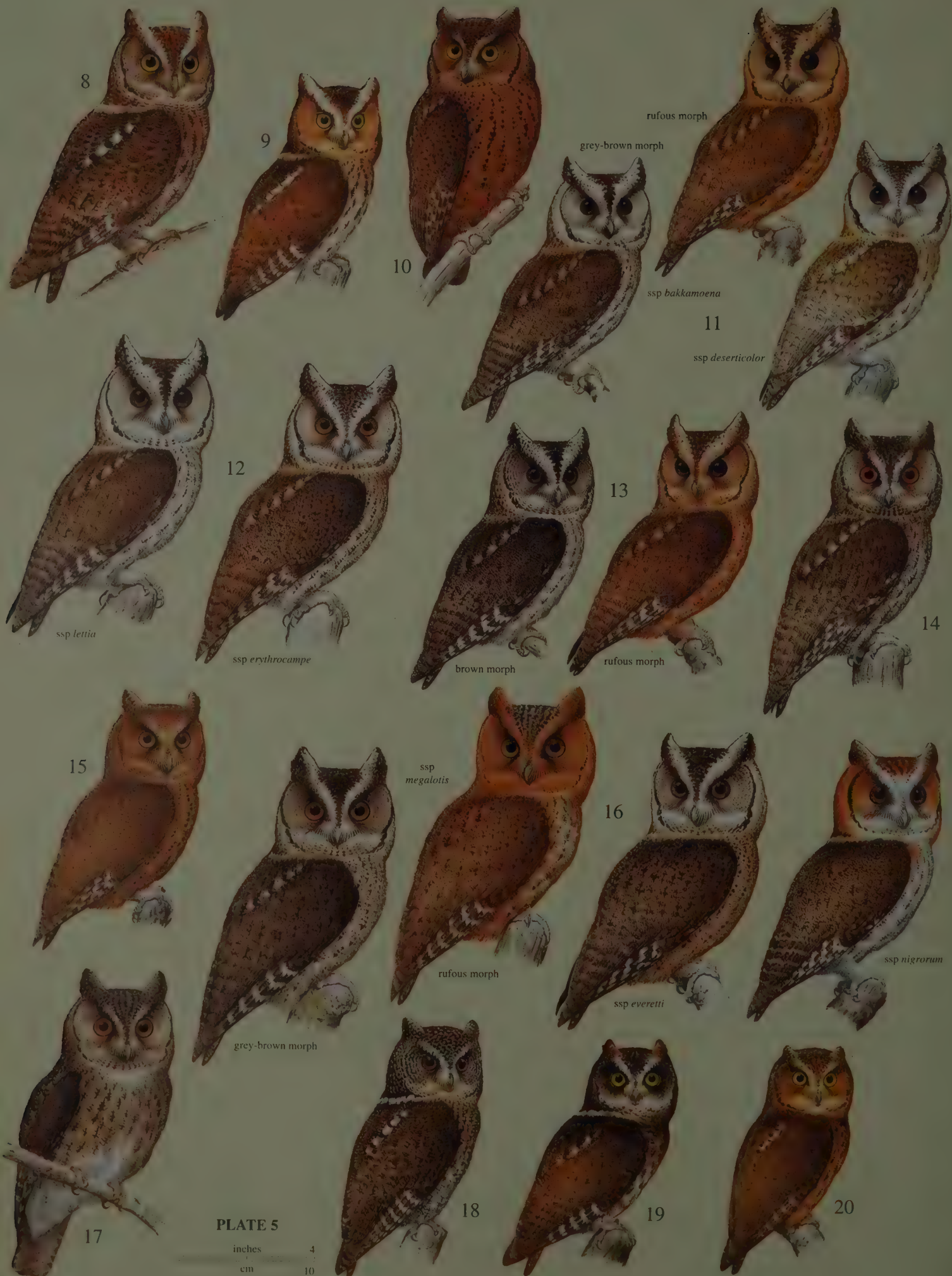
Breeding. Little recorded information regarding breeding in all but India and Pakistan. Lays Mar-Jun in Pakistan to NE India. Nest in unlined hollow in tree trunk, either natural or an abandoned woodpecker or barbet hole, usually 2-7 m above ground. 2-3 (2-5) eggs; incubation and fledging periods unrecorded.

Movements. Sedentary in most of range, but descends into warmer valleys of Himalayas in winter.

Status and Conservation. Not globally threatened. CITES II. Reasonably common throughout range. Locally common from Pakistan across to Myanmar, but scarce in Bangladesh; described as relatively abundant in mountains of Thailand, and common in Malay Peninsula and S Vietnam, but uncommon in Borneo and Sumatra. Occurs in a series of protected areas throughout its range, such as Doi Chiang Dao Wildlife Sanctuary in N Thailand. Hsitou (Chitou) Forest Recrea-

tion Area in Taiwan. Kerinci-Seblat National Park in Sumatra and Mount Kinabalu National Park in Sabah, Borneo; frequently recorded at Fraser's Hill, peninsular Malaysia. Fairly adaptable; fact that species will occupy areas of dense regenerating growth at disturbed forest edge should aid its survival.

Bibliography. Ali & Ripley (1981), Ali *et al.* (1996), van Balen (1997), Collar & Andrew (1988), Deignan (1945), Delacour (1947), Duckworth & Hedges (1998), Étchécopar & Hue (1978), Glenister (1951), Grimmer *et al.* (1998), Holmes (1996), Inskipp, C. & Inskipp (1991), Inskipp, T. *et al.* (1996), Lekagul & Round (1991), MacKinnon & Philipps (1993), van Marle & Voous (1988), Marshall (1978), Medway & Wells (1976), Meyer de Schauensee & Ripley (1940), Ripley (1982), Roberts (1991), Smythies (1981, 1986), Stepanyan (1995), Voous (1988), Wang Sung (1998), Wells (1999), Zhao Zhengjie (1995).



8. Rajah Scops-owl

Otus brookii

French: Petit-duc radjah **German:** Radschaeule
Other common names: Brooke's/Rajah Brooke's Scops-owl

Spanish: Autillo Raja

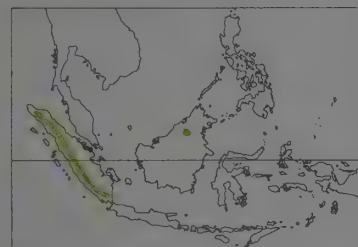
Taxonomy. *Scops brookii* Sharpe, 1892, Mount Dulit, Sarawak, Borneo. Probably forms superspecies with *O. angelinae*. Has been considered conspecific with latter, but the two differ in morphology and possibly in behaviour. Two subspecies recognized.

Subspecies and Distribution.

O. b. solokensis (Hartert, 1893) - Sumatra.

O. b. brookii (Sharpe, 1892) - Borneo.

Specimen collected in E Java (Ijen) assigned to this species, but identity disputed; may belong to another species of *Otus*.



Descriptive notes. c. 23 cm. Brown overall; prominent ear-tufts with white on inner side; upperparts rusty-brown, heavily marked with dark bars and black streaks, with some cream spots; conspicuous white collars on hindneck and across mantle; scapulars with black-tipped white spots; breast lighter rufous and cream with black streaks; tarsus heavily feathered; iris yellow; bill and feet yellow. Distinguished from *O. bakkamoena* by yellow eyes, distinct double collar and larger size. Juvenile nominate undescribed. Race *solokensis* with more yellow tone to plumage; juvenile dark rufous and barred above, spotted below. **Voice.** Clear, monotonous note, described as explosive, "whaooo", followed by single or paired notes, repeated for up to 1 minute; also 2-4 "gwoou" notes, apparently in flight.

Habitat. Montane rainforest, primarily between 1200 m and 2400 m; perhaps only in the subtropical zones within its range.

Food and Feeding. Little information; primarily insects, especially Coleoptera and Orthoptera, also moths; once a frog.

Breeding. Parents accompanying 2 fledglings in Jul; no other information.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Bornean Mountains EBA and Sumatra and Peninsular Malaysia EBA. Considered rare; possibly more widespread, but few observations within its known range. In Borneo, recorded only from Mt Dulit (Sarawak); in Sumatra, recorded from Gunung Kerinci and may possibly occur throughout the Barisan Range, but very few sightings and no indication that it is anything other than a very rare species. If Javan specimen of this species, then clearly extremely rare there, as no other records. Conservation status probably in need of revision.

Bibliography. Andrew (1992), Holmes (1996), MacKinnon (1988), MacKinnon & Philipps (1993), van Marle & Voous (1988), Marshall (1978), Smythies (1981), Stattersfield *et al.* (1998), Sujatnika *et al.* (1995), Tobias (1995).

9. Javan Scops-owl

Otus angelinae

French: Petit-duc de Java **German:** Angelinaeule **Spanish:** Autillo de Java
Other common names: Angelina's Scops-owl, Greater Sunda Scops-owl

Taxonomy. *Pisorhina angelinae* Finsch, 1912, Pangerango Mountain, 6000 feet [c. 2000 m], Java. Probably forms superspecies with *O. brookii*. Sometimes treated as conspecific with latter or with *O. spilocephalus* or, alternatively, as including race *vandewateri* of latter, but differs in morphology and also in far less vocal habits. Monotypic.

Distribution. W Java.



Descriptive notes. c. 16-18 cm; 70-90 g. Light rusty-brown facial disc, with prominent white eyebrows extending into ear-tufts; upperparts brown or rufous-brown, normally with rusty-buff hindneck-collar, and whitish scapular stripe; flight-feathers barred; underside whitish to pale buff with pronounced black streaks superimposed on faint rufous vermiculations; tarsus feathered to toes; iris golden-yellow; feet and bill yellowish-fleshy. Distinguished from *O. spilocephalus* by more prominent white eyebrows and ear-tufts, and golden rather than greenish-yellow iris. Juvenile somewhat darker and more barred and vermiculated, also with

yellowish markings on outer webs of primaries and yellowish bands on underside of tail. **Voice.** Far less vocal than *O. spilocephalus*, and often habitually silent. Main call, e.g. in alarm, an explosive "poo-poo" with short interval of c. 0.5 seconds between the notes, second note lower, repeated several times; contact call hissing "tch-tschschsch"; male also produces low, soft comfort call, "wook-wook".

Habitat. Frequents primary montane forest with well-developed understorey between 1500 m and 2500 m, but recorded as low as 1000 m; also seen in rainforest with upper canopy 40-55 m in height, and comprised of *Altingia*, *Quercus*, *Castanopsis* and *Ficus*. Prefers the lower and middle canopy layers, in which there is a wider variety of tree species. Occasionally roosts in rather exposed situations.

Food and Feeding. Primarily insects, including beetles, grasshoppers and crickets, and especially mantids; occasional reports of small lizards and snakes being taken. Snatches prey from trunk or foliage, or from ground.

Breeding. Families with two fledglings observed in Jul; no other information.

Movements. Sedentary.

Status and Conservation. VULNERABLE. CITES II. Restricted-range species: present in Java and Bali Forests EBA. Known only from two localities in W Java, Gunung Gede/Pangrango National Park and Gunung Tangkubanprahu. Considered rare by most authors, but in light of success obtained through mist-netting also speculated that it may be more common within its restricted range; this species' secretive behaviour and taciturn habits make any proper assessment of its population very difficult. Threats to its survival are unclear.

Bibliography. Andrew (1985, 1992), Andrew & Milton (1988), van Balen (1992), Becking (1994), Collar & Andrew (1988), Collar *et al.* (1994), Inskipp *et al.* (1996), Kuroda (1936), MacKinnon (1988), MacKinnon & Philipps (1993), Marshall (1978), Stattersfield *et al.* (1998), Sujatnika *et al.* (1995).

10. Mentawai Scops-owl

Otus mentawi

French: Petit-duc des Mentawai **German:** Mentawi-Zwergohreule **Spanish:** Autillo de las Mentawai
Other common names: Sipora Scops-owl

Taxonomy. *Otus bakkamoena mentawi* Chasen and Kloss, 1926, Sipora Island.

Probably forms superspecies with *O. bakkamoena*, *O. letitia*, *O. lempiji*, *O. semitorques*, *O. fuliginosus* and *O. megalotis*. Has sometimes been treated as conspecific with *O. bakkamoena*, *O. lempiji*, *O. sunia* or *O. manadensis*, but vocalizations distinct. Monotypic.

Distribution. Mentawai Is (Siberut to S Pagai), off W Sumatra.



Descriptive notes. 20 cm. Occurs in rufous-chestnut and blackish-brown morphs. Prominent ear-tufts and eyebrows whitish with dark mottles; upperparts with dark blotches and streaks; underparts paler, with black shaft streaks enclosing small whitish ocelli; tarsi feathered to toes; yellow iris; horn-coloured bill; grey toes. Lacks white collar of *O. bakkamoena*. Juvenile undescribed. **Voice.** Male gives series of "po-po" calls, ending in descending sequence of 7-8 "po" notes; also gruff honking noises, varying in pitch and inflection; duets, with female's higher-pitched quavering notes following male's "po-po..."

until songs synchronous, longest sequence c. 2 minutes.

Habitat. Lowland rainforest and secondary growth; sometimes near settlements; in villages, not infrequently perches on exposed branches.

Food and Feeding. Apparently insects.

Breeding. No information.

Movements. Presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Status poorly known; appears to be rare and rather patchily distributed, but possibly locally common. Continuing destruction of forest habitat a likely threat, but species' apparent ability to tolerate human-altered habitats, e.g. villages and their surroundings, may aid its long-term survival.

Bibliography. Andrew (1992), Chasen & Kloss (1926), Deignan (1950b), Holmes, D.A. (1994a), Inskipp *et al.* (1996), MacKinnon & Philipps (1993), van Marle & Voous (1988), Marshall (1978), Riley (1929), Stattersfield *et al.* (1998).

11. Indian Scops-owl

Otus bakkamoena

French: Petit-duc à collier **German:** Indien-Zwergohreule **Spanish:** Autillo Indio
Other common names: Collared Scops-owl(!), Oriental Screech-owl

Taxonomy. *Otus bakkamoena* Pennant, 1769, Sri Lanka.

Probably forms superspecies with *O. mentawi*, *O. letitia*, *O. lempiji*, *O. semitorques*, *O. fuliginosus* and *O. megalotis*. Taxonomy complex and controversial, with various treatments by different authors: often considered to include one, or several, or all of above-mentioned species as races; sometimes regarded as conspecific with *O. lempiji*; or as monotypic, with all other currently recognized races placed with *O. letitia*; boundaries between all taxa poorly understood. Present treatment based mainly on vocalizations. Five subspecies recognized.

Subspecies and Distribution.

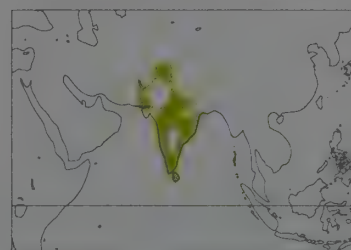
O. b. plumipes (Hume, 1870) - W Himalayas, from N Pakistan E to Nepal border.

O. b. deserticolor Ticehurst, 1922 - S Pakistan; possibly SE Iran; old record from Oman probably erroneous.

O. b. gangeticus Ticehurst, 1922 - NW India to lowland Nepal.

O. b. marathae Ticehurst, 1922 - C India, E to about S West Bengal.

O. b. bakkamoena Pennant, 1769 - SW & SE India and Sri Lanka.



Descriptive notes. c. 20 cm; male wingspan 60-5-61 cm, female 66 cm; 125-150 g. Occurs in grey-brown and rufous morphs; latter generally with distinct ochre tinge, commoner in S populations. Facial disc light greyish or rufous; forehead, eyebrows and conspicuous long ear-tufts much paler, whitish, with crown mottled blackish; upperparts mottled and spotted dark, with distinct buff collar on hindneck and another on nape, but indistinct scapular spots; underparts grey-buff to rufous-buff, with dark shaft streaks and vermiculations; iris generally brown; legs may be feathered to base of toes; bill and feet horn-coloured. Juvenile pale grey

to yellowish-brown, barred brown all over. Races vary in general coloration: *gangeticus* paler than nominate; *marathae* more grey, less rufous; *plumipes* somewhat darker; *deserticolor* much paler, pale sandy, with more golden eyes. Voice. Male gives quiet, frog-like, questioning "wuk?" or "whut?", repeated at irregular intervals, usually of 4-6 seconds; female call lower; rising series of chattering calls also heard.

Habitat. Forest, groves near towns and in cultivated areas, well-timbered gardens, orchards with shade trees; occasionally more open country with plenty of trees; also irrigated plantations and riverine forest in dry parts of Pakistan; noted nesting at edges of rubber and tea plantations in Sri Lanka. Nocturnal, hides in hollows or dense tree foliage during day. From plains up to c. 2130 m in Pakistan; to 1200 m in peninsular India, locally to 2400 m in E Himalayas; mostly lowlands and lower hills in Sri Lanka.

Food and Feeding. Primarily beetles, grasshoppers and other insects, including moth larvae; occasionally rodents, small birds and lizards, perhaps rarely bats.

Breeding. Lays Dec-May, mostly in later months, often during rainiest season in S of range; in Pakistan, nestlings found in Mar and Apr, also eggs in Apr. Nest generally in natural hollow in tree trunk, sometimes in abandoned building near habitation. 3-5 eggs; incubation possibly 25-27 days.

Movements. Resident in most of range; some movement to lower levels in winter, and variable nomadic movements according to food supply.

Status and Conservation. Not globally threatened. CITES II. Widespread and locally common; not really rare anywhere within range. Although rather retiring and rarely seen, described as common in Pakistan and Sri Lanka, frequent in Bhutan, locally common in Bangladesh, and at least locally common in India.

Bibliography. Ali (1996), Ali & Ripley (1981), Beaman (1994), Chakravarthy & Purna Chandra Tejasvi (1992), Daniels (1997), Deignan (1950b), Grimmett *et al.* (1998), Henry (1998), Hùe & Échécopar (1970), Inskipp *et al.* (1996), Khajuria (1970), Kotagama & Fernando (1994), Lamsfuss (1998), Marshall (1978), Mukherjee (1995), Phillips (1978), Ripley (1982), Roberts (1991), Roberts & King (1986), Roonwal (1950), Saha & Dasgupta (1992), Sugathan & Varghese (1996), Voous (1988), Wijesinghe (1994).

12. Collared Scops-owl

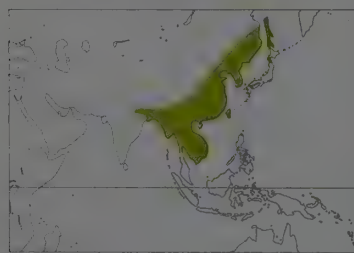
Otus lettia

French: Petit-duc indien **German:** Halsband-Zwergohreule **Spanish:** Autillo Chino
Other common names: Indian Scops-owl(!)

Taxonomy. *Scops lettia* Hodgson, 1836, Nepal. Probably forms superspecies with *O. mentawi*, *O. bakkamoena*, *O. lempiji*, *O. semitorques*, *O. fuliginosus* and *O. megalotis*. Previously considered a race of *O. bakkamoena*, including under synonyms *manipurensis* and *albioniger*, a treatment still preferred by many authors, and may intergrade with that species in Nepal; also, considered by some conspecific with *O. lempiji*. Differences in vocalizations, however, suggest specific status. Position of race *ussuriensis* unclear, but plumage features, eye colour and vocalizations close to *O. semitorques* and possibly better placed with latter; Indochinese population, tentatively included in nominate, may be closer to *erythrocampe*. Proposed race *aurorae* from N China included in *ussuriensis*. Five subspecies recognized.

Subspecies and Distribution.

O. l. lettia (Hodgson, 1836) - E Nepal, E India (West Bengal) and Bangladesh, E to Assam, Myanmar, Thailand (except S peninsula) and Indochina.
O. l. erythrocampe (Swinhoe, 1874) - SE China.
O. l. ussuriensis (Buturlin, 1910) - Sakhalin, Ussuriland and NE China.
O. l. glabripes (Swinhoe, 1870) - Taiwan.
O. l. umbratilis (Swinhoe, 1870) - Hainan I.



Descriptive notes. 23-25 cm; 100-170 g. Occurs in grey-brown and rufous morphs. Facial disc greyish to light rufous, with buff eyebrows and inner webs of ear-tufts, latter rather small but conspicuous when raised; upperside grey-brown or rufous-brown, dark-mottled and with few whitish spots, and pale collar on back of neck; chin and throat pale, barred or mottled with black, breast pale greyish-buff or rufous with black streaks; tarsus feathered; iris yellowish-brown; bill green to horn with blackish tip, lower mandible yellow; feet and claws fleshy-grey to dark olive. Differs from similar *O. semitorques* in eye colour and voice.

Juvenile more barred. Races not very well marked: *erythrocampe* generally less grey, more brown and buff, with dark yellow to golden-brown eyes; *glabripes* paler, *umbratilis* darker; *ussuriensis* with orange tinge to eyes. Voice. Male gives single mellow "buoo", inflected downwards, repeated at longish intervals of 12-20 seconds; female similar but higher-pitched, more mewing; courtship duets can continue for 15 minutes or longer. Also chattering series in alarm. Race *ussuriensis* said to give "koog koog" call at extremely long intervals in breeding season.

Habitat. Sal, deciduous and evergreen forest, secondary growth, also open scrub near cultivation, open areas with stands of trees and bamboo, and gardens in towns and villages; open mixed forest with moderate understorey in E Russia. Considered primarily a submontane species in E Himalayas, where occurs at up to 2400 m, but elsewhere in range equally frequent from lowland plains to at least 2200 m.

Food and Feeding. Insects (especially beetles and grasshoppers); diet also includes moderate proportion of vertebrates, such as rodents, small birds and lizards. In NE of range, breeding-season concentrations of these owls in areas with rodent plagues indicate that small mammals taken locally in large numbers.

Breeding. Feb-Apr/May; some evidence that breeding season may be longer; in Ussuriland, young leave nest in Jul. Nest a natural hollow or woodpecker hole 2-5 m from ground, sometimes higher, in either living tree trunk or, perhaps more commonly, a snag. Usually 3-5 eggs; reported that both parents may share in incubation duties.

Movements. Generally resident, with some local movement from higher-lying areas to lower levels in winter. Many individuals of N populations (*ussuriensis*) migrate in autumn to Korea and N China, some possibly moving farther S; recorded as vagrant in Japan (Honshu).

Status and Conservation. Not globally threatened. CITES II. Described as very common in parts of range, e.g. Thailand and Myanmar, and locally frequent in E Himalayas; race *ussuriensis* said to be rather scarce. Does not shun man's presence, and appears able to live in association with agricultural development, so long as some trees available; by no means uncommon in suburban areas, and also tolerates more urbanized habitats in places. No obvious threats.

Bibliography. Ali (1996), Ali & Ripley (1981), Ali *et al.* (1996), Deignan (1950b), Échécopar & Hùe (1978), Flint *et al.* (1984), Grimmett *et al.* (1998), Inskipp, C. & Inskipp (1991), Inskipp, T. *et al.* (1996), Knystautas

(1993), Majumdar *et al.* (1992), Marshall (1978), Ripley (1982), Smythies (1986), Stepanyan (1990, 1995), Voous (1988), Zhao Zhengjie (1995).

13. Sunda Scops-owl

Otus lempiji

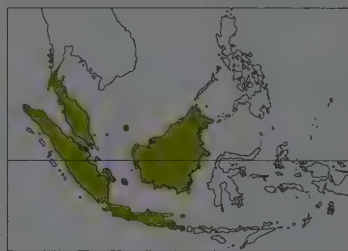
French: Petit-duc de Horsfield **German:** Sunda-Zwergohreule **Spanish:** Autillo de la Sonda
Other common names: Collared Scops-owl(!)

Taxonomy. *Srix* [sic] *Lempiji* Horsfield, 1821, Java.

Probably forms superspecies with *O. mentawi*, *O. bakkamoena*, *O. lettia*, *O. semitorques*, *O. fuliginosus* and *O. megalotis*. Frequently treated as race of *O. bakkamoena*, and sometimes considered to include as race or to be conspecific with *O. lettia*, but vocalizations distinct. Race *cnephaeus* apparently differs vocally, may be separate species; *condorensis* doubtfully distinct from nominate. Six subspecies recognized.

Subspecies and Distribution.

O. l. condorensis Kloss, 1930 - S peninsular Thailand below Isthmus of Kra.
O. l. lempiji (Horsfield, 1821) - Malay Peninsula (except S), S Sumatra, Bangka, Belitung, Java, Bali, N Natuna Is, Borneo (except N).
O. l. cnephaeus Deignan, 1950 - S Malay Peninsula.
O. l. hypnoides Deignan, 1950 - N & C Sumatra.
O. l. lemorum Deignan, 1957 - N Borneo.
O. l. kangeanus Mayr, 1938 - Kangean Is.



Descriptive notes. c. 20 cm; 100-120 g. Occurs in grey-brown and rufous morphs. Facial disc greyish to light rufous-buff with blackish border; buffy-whitish forehead, eyebrows and long ear-tufts, latter edged black, contrast sharply with blackish to dark brown crown; upperparts dull brown to greyish, densely marked with black blotches and buff spots, with indistinct pale buff or sandy nuchal collar; underparts buffy grey-brown to cinnamon, with dark shaft streaks and thin broken vermiculations; tarsus fully feathered; iris dark brown, but said rarely to be bright yellow; bill and feet ivory-white to pale yellow. Differs

from very similar *O. semitorques* in eye colour and voice. Juvenile generally more brownish-buff and more barred, especially on crown. Races poorly defined: *hypnoides* tends to be darker, especially rufous morph; *cnephaeus* somewhat smaller and with different call. Voice. Male utters soft, upward-inflected "wooup", repeated at intervals of 10-15 seconds, often continued for several periods; female similar, but slightly higher-pitched; duets in breeding season, with all calls equally spaced. Race *cnephaeus* said to give uninflected call, with intervals between calls longer.

Habitat. Second-growth evergreen and deciduous forest, forest edge, plantations, open areas with scattered trees, parks, villages, well-wooded gardens, and tree-lined suburban and urban streets; adaptable, readily accepts human-altered habitats; avoids primary forest. From sea-level to 1000 m, occasionally to 1600 m, locally to c. 2000 m.

Food and Feeding. Mostly insects, especially large beetles, Orthoptera, Lepidoptera and mantids; occasionally small birds, e.g. munias (*Lonchura*), perhaps mainly nestlings, and mice. Hunts from a perch, including roof of house or village hut, dropping on to prey on or near ground.

Breeding. Lays mainly Jan-Apr, occasionally later; fledgling just off nest in mid Jun in Borneo. Nest in natural hole in tree, sometimes in other hollow area formed by e.g. dead palm leaves; nest also recorded in uninhabited houses. 2 eggs, rarely 3; chick down white (Malay Peninsula), greyish (Java) or rufous.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Considered common in Malaysia and fairly common to very common throughout Greater Sundas. In some parts of its range, such as Sumatra, described as the most common strigid; no reports indicating population declines or scarcity. Apparent attraction to cultivations and human-populated areas advantageous to its survival; would appear to benefit from conversion of forested land to agricultural uses, enabling possible range expansion.

Bibliography. Bucknill & Chasen (1990), Deignan (1945, 1950b), Delacour (1947), Glenister (1951), Hellebrekers & Hoogerwerf (1967), Hoogerwerf (1949a), Inskipp *et al.* (1996), Lekagul & Round (1991), MacKinnon (1988), MacKinnon & Phillips (1993), Madoc (1976), van Marle & Voous (1988), Marshall (1978), Medway & Wells (1976), Mees (1986), Riley (1938), Roonwal (1950), Smythies (1981, 1986), Voous (1988), Wells (1999).

14. Japanese Scops-owl

Otus semitorques

French: Petit-duc du Japon **German:** Japan-Zwergohreule **Spanish:** Autillo Japonés

Taxonomy. *Otus semitorques* Temminck and Schlegel, 1844, Kyushu, Japan.

Probably forms superspecies with *O. mentawi*, *O. bakkamoena*, *O. lettia*, *O. lempiji*, *O. fuliginosus* and *O. megalotis*. Formerly treated as subspecies of highly variable *O. bakkamoena*, but significant differences in vocalizations, as well in eye colour, indicate separate species. Sometimes considered to include race *ussuriensis* of *O. lettia*, which closer to present species in voice and plumage characters, and also intermediate in eye colour; possibly better included as race of present species. Two subspecies recognized.

Subspecies and Distribution.

O. s. semitorques Temminck & Schlegel, 1844 - S Kuril Is (Urup S to Kunashir), and Hokkaido S to Yakushima, including Sado, Tsushima, Goto Is and Yakushima.
O. s. pryeri (Gurney, 1889) - S Izu Is (Hachijo) and S Ryukyu Is (Okinawa to Iriomote).

Descriptive notes. 23-25 cm; wingspan 60-66 cm; c. 130 g. Relatively long, pointed wings, with primary P7 longest. Facial disc pale grey-brown with dark speckles; eyebrows and prominent ear-tufts whitish; upperparts grey-brown, tinged sandy, with coarse blackish and buff markings; well-defined lighter nuchal band, with less distinct pale occipital patch above it; flight-feathers brown with light pale bars, tail with 7-8 dark brown marbled bands; chin and sides of throat sometimes whitish; underparts light greyish-buff, streaked dark, and with delicate transverse pencil-lines; tarsi and toes feathered; iris orange to red. Differs from *O. bakkamoena*, *O. lettia* and *O. lempiji* in wing shape and length, red eyes and voice; extremely similar to race *ussuriensis* of *O. lettia*, but somewhat darker. Juvenile greyish-buff and distinctly barred all over. Race *pryeri* less grey, more rusty-coloured, toes unfeathered, eyes orange-yellow. Voice. Male gives deep "whook", regularly



repeated at long intervals; many other calls described, e.g. "koo" or "kwe" notes, also repeated "kwee-kwee" or "pew-u, pew-u".

Habitat. Lowland forest, wooded plains and forested hillsides, up to 900 m above sea-level; in winter, also parks and gardens, including those in towns and cities.

Food and Feeding. Mostly insects, small rodents (especially voles and mice) and spiders; occasionally takes small birds, frogs, lizards and crustaceans.

Breeding. Lays May-Jul. Nest in natural tree cavity; 4-5 eggs. Incubation and fledging periods not reported.

Movements. Resident, nomadic and migratory; moves to lower altitudes in winter. Autumn influx in SE Hokkaido, presumably of birds from Kurils; other N birds may move S to plains, coastal areas or even cities; winter visitor to S coastal regions of Honshu, e.g. to Tokyo area during Oct-Mar and to Yamanashi-ken during Nov-Apr.

Status and Conservation. Not globally threatened. CITES II. Locally common; very common in Tsushima; fairly common in Kyushu, Shikoku, Honshu and Sado; less common in Hokkaido. Race *pyerri* poorly known; although reported as abundant in Iriomote, this not substantiated by later observations. No obvious threats, and appears able to live in proximity to man.

Bibliography. Austin & Kuroda (1953), Brazil (1991), Brazil & Yamamoto (1989a), Deignan (1950b), Flint *et al.* (1984), Higuchi & Momose (1980), Marshall (1978), Sonobe (1982), Stepanyan (1990), Voous (1988), Zhao Zhengjie (1995).

15. Palawan Scops-owl

Otus fuliginosus

French: Petit-duc de Palawan **German:** Palawan-Zwergohreule **Spanish:** Autillo de Palawan

Taxonomy. *Scops fuliginosa* Sharpe, 1888, vicinity of Puerto Princesa, Palawan.

Probably forms superspecies with *O. mentawi*, *O. bakkamoena*, *O. lettia*, *O. lempiji*, *O. semitorques* and *O. megalotis*. Formerly treated as subspecies of *O. bakkamoena*, but vocalizations distinct from latter's. Monotypic.

Distribution. Palawan I, in SW Philippines.



Descriptive notes. c. 19-20 cm. Conspicuous ear-tufts; light rufous facial disc; upperparts dark reddish-brown, finely vermiculated black; reduced pale collar on hindneck; pale buffy-brown to chestnut below, with dark streaks and vermiculations; iris pale orange-brown to yellowish-ochre; bill horn; bare toes greyish-yellow. Lacks chestnut on back, otherwise closely resembles the larger *O. mentawi*; differs from *O. megalotis* in smaller size, less prominent nuchal collar. Juvenile undescribed. **Voice.** Male call described as deep, croaking rasp, "krarr-kuarr", repeated at short intervals.

Habitat. Lowland forest, and mixed cultivation with trees.

Food and Feeding. No information; presumably insects.

Breeding. No information.

Movements. Sedentary.

Status and Conservation. VULNERABLE. CITES II. Restricted-range species; present in Palawan EBA. Said to be very rare. Most recent records from St Paul Subterranean National Park, where perhaps locally not uncommon, and from Iwahig and Balsahan. Threatened by lowland deforestation, which is increasing in extent on Palawan.

Bibliography. Anon. (1997b), Collar *et al.* (1994), Deignan (1950b), Dickinson *et al.* (1991), Inskipp *et al.* (1996), Marshall (1978), McGregor (1909-1910), duPont (1971), Stattersfield *et al.* (1998), Voous (1988).

16. Philippine Scops-owl

Otus megalotis

French: Petit-duc de Luzon **German:** Philippinen-Zwergohreule **Spanish:** Autillo Filipino
Other common names: Whitehead's Scops-owl, Luzon Collared Scops-owl

Taxonomy. *Scops megalotis* Walden, 1875, probably Manila.

Probably forms superspecies with *O. mentawi*, *O. bakkamoena*, *O. lettia*, *O. lempiji*, *O. semitorques* and *O. fuliginosus*. Older name *O. whiteheadi* sometimes still used, now rejected. Formerly treated as conspecific with *O. bakkamoena*, but shown to be vocally distinct. Race *boholensis* doubtfully distinct from *everetti*. Four subspecies recognized.

Subspecies and Distribution.

O. m. megalotis (Walden, 1875) - Luzon, Marinduque and Catanduanes.

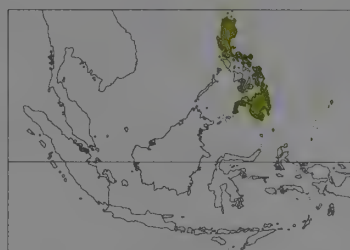
O. m. everetti (Tweeddale, 1879) - Samar, Biliran, Leyte, Mindanao and Basilan.

O. m. nigrorum Rand, 1950 - Negros.

O. m. boholensis McGregor, 1907 - Bohol.

Descriptive notes. 23-28 cm; c. 200-300 g. With *O. sagittatus*, the largest of the Old World scops-owls. Occurs in grey-brown and rufous morphs. Grey-brown morph deep brown or brownish-olive above with buff vermiculations, black-tipped pale feathers on hindneck forming collar, whitish eyebrows, underparts buffish-grey with some broad black shaft markings and few thin cross-lines; rufous phase brownish-red above, generally buffy-yellow below; both morphs with barred wings and tail; tarsus feathered to toes; iris golden-brown or orange-brown; bill light brown, tipped with white; feet dull white to yellow-brown. Differentiated from *O. bakkamoena* by comparatively larger size. Juvenile similar to respective adult morph but more barred, rufous morph more deeply cinnamon than adult. Race *everetti* smaller than nominate, with tarsal feathering stopping short of foot; *nigrorum* very distinct and smaller still, with bright rusty head and whiter underparts. **Voice.** A loud, sudden series of 3-6 ascending notes on falling scale, similar to *O. lempiji* call but notes longer; also powerful "oik oik oik oik", with marked interval between each note.

Habitat. Tropical forest and secondary woodland, generally in denser parts; occurs mostly up to c. 1200 m, but in SE Luzon noted between 450 m and 1550 m on Mt Isarog. Noted roosting among root system of partly upturned dead tree.



Food and Feeding. Stomach contents revealed only insects.

Breeding. Males captured in Mar in or approaching breeding condition; young fledgling in Feb in Luzon; juveniles in May in Negros, estimated to have hatched Jan-Feb; possibly lays from Dec/Jan onwards. Possibly 3-4 eggs, but family party with just 1 young recorded.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Few reliable data. Reports vary from probably endangered to widely distributed (on Mt Isarog), but very little is known about this species. May be found to be locally

common. Since it appears to prefer densely wooded habitats, forest clearance and destruction presumably a threat at least in some parts of range.

Bibliography. Amadon & duPont (1970), Brooks, Evans *et al.* (1992), Brooks, Dutton *et al.* (1996), Danielsen *et al.* (1994), Deignan (1950b), Delacour & Mayr (1946), Dickinson, Kennedy & Parkes (1991), Dickinson, Kennedy, Read & Rozendaal (1989), Gilliard (1950a), Goodman & Gonzales (1989, 1990), Inskipp *et al.* (1996), Marshall (1978), McGregor (1909-1910), Oliver & Wirth (1996), duPont (1971), duPont & Rabor (1973b), Rabor (1938a, 1977), Rand (1950), Rand & Rabor (1960), Voous (1988).

17. Wallace's Scops-owl

Otus silvicola

French: Petit-duc de Wallace **German:** Wallace-Zwergohreule **Spanish:** Autillo de Wallace
Other common names: Flores(!)/(Lesser) Sunda Scops-owl(!)

Taxonomy. *Scops silvicola* Wallace, 1864, Flores.

Relationships unclear; probably closest to the *O. bakkamoena* superspecies. Monotypic.

Distribution. Sumbawa and Flores, in Lesser Sundas.



Descriptive notes. c. 23-25 cm. Facial disc fairly uniform tan, with paler eyebrows; long ear-tufts mottled brown and buff; upperparts olive-brown, lightly vermiculated buffy-tan, with dark brown shaft streaks throughout; flight-feathers brown, with white bars darkening to tan near tips; tail finely barred buff; underparts barred brown and buffish-tan, with dark brown drop-like streaks, and diagnostic white patch across upper breast; tarsus feathered white to toes; dull orange-yellow eyes and yellow to greyish bill. Relatively similar to *O. semitorques*. Juvenile generally paler, more rufous, with less distinct patterning. **Voice.** Territorial call steady series of c. 10 (up to 18) deep "whumph" notes on same pitch; at dawn, 4-5 songs at 3-minute intervals; also gruff "row" call, repeated irregularly.

Habitat. Semi-evergreen rainforest, forest edge, and submontane forest with bamboo thickets; more rarely moist deciduous forest, also wooded areas around farms; locally in urban areas, e.g. recorded in town of Ruteng, on Flores. From 350 m to 1600 m.

Food and Feeding. No information.

Breeding. Virtually unknown; probably lays during May.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Northern Nusa Tenggara EBA. Currently considered Near-threatened. Probably under-recorded; considered common. Fairly adaptable, and able to live in variety of habitats, but appears to be most numerous in semi-evergreen forest below 1450 m; this habitat increasingly scarce, and forest destruction thus a long-term threat.

Bibliography. Andrew (1992), Buck (1988), Butchart *et al.* (1993, 1996), Coates & Bishop (1997), Holmes (1993), Jepson & Monk (1995), Johnstone *et al.* (1996), Marshall (1978), Paynter (1963), Rensch (1931), Stattersfield *et al.* (1998), Sujatnika *et al.* (1995), White & Bruce (1986).

18. Mindanao Scops-owl

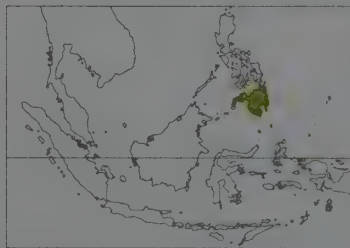
Otus mirus

French: Petit-duc de Mindanao **German:** Mindanaoeule **Spanish:** Autillo de Mindanao

Taxonomy. *Otus scops mirus* Ripley and Rabor, 1968, Hilong Hilong Peak, Agusan Province, Mindanao.

Probably forms superspecies with *O. longicornis*. Formerly treated as race of either *O. sunia* or *O. scops*, but differs greatly from both in morphology and vocalizations. Monotypic.

Distribution. Mindanao I, in S Philippines.



Descriptive notes. 19-20 cm. A dark, boldly marked species. Facial disc pale greyish-brown with indistinct rings; eyebrows and inner part of smallish ear-tufts whitish; upperparts greyish-brown, heavily blotched blackish and lightly with rufous; white spots form conspicuous hindneck-collar; partly white scapulars form fairly prominent line; wings and tail prominently barred; underparts mainly white with strong pattern of heavy black lines and finer cross-lines; tarsus bare for distal third; iris brown to yellow; bill greenish-grey; lower tarsus and toes grey to pale yellow-grey. Juvenile unknown. **Voice.** Said to utter soft double

notes, recalling pigeon or dove (Columbidae).

Habitat. Montane rainforest.

Food and Feeding. No information.

Breeding. No information.

Movements. Presumably resident.

Status and Conservation. VULNERABLE. CITES II. Restricted-range species: present in Mindanao and the Eastern Visayas EBA. Apparently rare in restricted range, and very few observations. Recorded only from Mt Apo and Mt Hilong-Hilong, and more recently from Mount Katanglad National Park and Sitio Siete. Continuing forest destruction at all three localities must pose serious threat to its survival.

Bibliography. Anon. (1997b), Collar *et al.* (1994), Dickinson *et al.* (1991), Inskipp *et al.* (1996), Marshall (1978), Ripley & Rabor (1968), Stattersfield *et al.* (1998).

19. Luzon Scops-owl

Otus longicornis

French: Petit-duc longicorne

German: Luzoneule

Spanish: Autillo de Luzón

Other common names: Luzon Slender-billed Scops-owl

Taxonomy. *Scops longicornis* Ogilvie-Grant, 1894, mountains of northern Luzon.

Forms part of assemblage referred to as subgenus *Otus*. Probably forms superspecies with *O. mirus*. Previously treated as race of *O. scops* or *O. spilocephalus*, but differs from both in morphology and apparently in vocalizations. Monotypic.

Distribution. Luzon, in N Philippines.



Descriptive notes. c. 19 cm. Frosted facial trim, white eyebrows, long loreal plumes barred white with black tips, long ear-tufts with some rufous colouring, ear-coverts barred white, blackish-brown and rufous; pale or white collar, narrower on hindneck than on breast; upperparts bright rufous-buff, streaked and with irregular dark bars on each feather; chin and throat whitish, throat feathers tipped with black; breast rufous, mottled with black and white, rest of underparts white with fulvous and rusty-brown mottling; tarsus feathered for roughly half length; iris yellow; bill slender, laterally compressed, dull green; lower tarsus

and toes whitish-flesh. Juvenile not described. **VOICE.** Said to give an odd, whistling "quop".

Habitat. Humid forest, generally in foothills and mountains, also in pine woodland; specimens collected from 360-1800 m; recently observed in lower montane forest at 700-1500 m.

Food and Feeding. Stomach contents included primarily insects.

Breeding. Nest with 3 chicks in May. Nest in tree hole. 2-3 eggs; chick with light grey down, this replaced by brown-barred grey.

Movements. Presumably resident.

Status and Conservation. VULNERABLE. CITES II. Restricted-range species: present in Luzon EBA. Evidently rare, and few reliable sightings. Recent records from Quezon National Park, near

Manila, and from Mt Cetaceo and Mt Dimalayag in Sierra Madre, in NE Luzon. Rarity attributed to habitat loss, and this seems likely to continue. Research needed on species' ecology and biology, in order to determine its conservation requirements.

Bibliography. Amadon & duPont (1970), Anon. (1997b), Collar *et al.* (1994), Danielsen *et al.* (1994), Dickinson *et al.* (1991), Goodman & Gonzales (1990), Hachisuka (1934), Inskipp *et al.* (1996), Marshall (1978), McGregor (1904, 1909-1910), Ogilvie-Grant (1894), Poulsen (1995), Stattersfield *et al.* (1998).

20. Mindoro Scops-owl

Otus mindorensis

French: Petit-duc de Mindoro

German: Mindoroeule

Spanish: Autillo de Mindoro

Taxonomy. *Scops mindorensis* Whitehead, 1899, highlands of Mindoro.

Relationships uncertain, but resembles some taxa of *O. mantananensis*. Formerly treated as race of *O. scops* or *O. sunia*, but very different from both in morphology. Birds in lowlands of W Mindoro recently attributed to this species, but differing vocally from other populations, now shown to be race *mindorensis* of *Ninox philippensis*. Monotypic.

Distribution. Mindoro, in NC Philippines.



Descriptive notes. 18-19 cm. Small, with overall plumage dull and finely marked; ear-tufts of moderate length and blotchy; upperparts brown with vague fine darker streaking and vermiculations; mainly buffy below with narrow dark streaks and inconspicuous dark and white barring; tertials essentially unbarred, while tail is narrowly banded; tarsi half feathered; claws small, weak, pale. Juvenile undescribed. **VOICE.** Male's call a short hoot, "who", repeated in series with intervals of 5 seconds or more.

Habitat. Montane forest above 870 m; roosts by day in dense foliage or in tree cavity.

Food and Feeding. Mostly insects.

Breeding. Type specimen, collected in Jan, had well-developed eggs; no other information.

Movements. Resident.

Status and Conservation. VULNERABLE. CITES II. Restricted-range species: present in Mindoro EBA. Apparently quite common in suitable habitat; in some areas, individuals spaced at no more than c. 150 m. Montane forest now greatly diminished in size, however, and confined to elevations above 870 m; continuing clearance operations reducing area of suitable habitat even further.

Bibliography. Anon. (1997b), Collar & Andrew (1988), Collar *et al.* (1994), Dickinson *et al.* (1991), Dutson *et al.* (1992), Evans, Dutson & Brooks (1993), Inskipp *et al.* (1996), Marshall (1978), McGregor (1909-1910), Oliver & Wirth (1996), Stattersfield *et al.* (1998).



21. Pallid Scops-owl

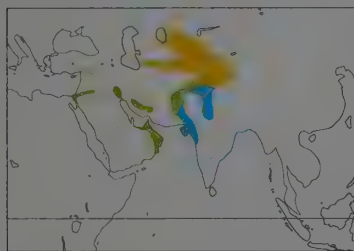
Otus brucei

French: Petit-duc de Bruce **German:** Streifenohreule **Spanish:** Autillo Persa
Other common names: Striated/Bruce's Scops-owl, Desert Screech-owl

Taxonomy. *Ephialtes Brucei* Hume, 1873, Rahuri, Ahmednagar, Maharashtra. Probably forms superspecies with *O. senegalensis*, *O. scops*, *O. sunia* and *O. flammeolus*. Has often been considered race of *O. scops* or *O. sunia*, but significant differences in voice and morphology, and no hybridization in areas of range overlap. Socotran form *socotranus* and Arabian *pamelae* currently placed with *O. senegalensis*, but sometimes included with present species, or may be specifically distinct. Geographical boundaries of races unclear, with apparent intergradation, and individuals showing intermediate characters (e.g. between *obsoletus* and *exiguus*); Turkish birds sometimes placed in *exiguus*; *obsoletus* and *semenowi* sometimes considered only intergrades between races. Four subspecies recognized.

Subspecies and Distribution.

O. b. brucei (Hume, 1873) - E Aral Sea to Kirgizia and Tajikistan.
O. b. obsoletus (Cabanis, 1875) - S Turkey, N Syria, N Iraq, Turkmeniya, Uzbekistan and N Afghanistan.
O. b. semenowi (Sarudny & Härms, 1902) - S Tajikistan and W China (E to C Tarim Basin) S to E Afghanistan and N Pakistan.
O. b. exiguus Mukherjee, 1958 - Israel (extinct as breeder), C & E Iraq, S Iran, Oman, S Afghanistan, W Pakistan.



Descriptive notes. 21 cm; wingspan 54-64 cm; c. 100-110 g. Pale scops-owl with distinct fine streaking and short ear-tufts. Facial disc pale buffish-white, with thin dark border and short whitish eyebrows; upperparts light greyish-brown with yellowish tinge, with sparse and fine black streaks, broader on crown and forehead, nape with light ochre patch, scapulars with blackish-edged white feathers; flight-feathers and tail thinly barred; below, paler and more heavily streaked with black, especially on centre of breast; tarsus fully feathered to base of toes; iris yellow; bill brownish-horn, yellowish at base of lower mandible; feet grey; claws dark horn, occasionally described as lead-coloured. Distinguished from all races of *O. scops* by paler appearance, plainer upperparts, lack of rufous coloration, absence of transverse patterning below. Juvenile paler, narrowly barred creamy and grey, shorter ear-tufts. Races differ mainly in plumage coloration, but much overlap: *semenowi* similar to nominate, but deeper ochre-yellow, streaks sometimes broader; *obsoletus* more sandy-buff, streaks narrower but sharp; *exiguus* greyer, streaks below weaker, more diffuse. Voice. Male territorial call a long series of low, hollow "whoop" or "who" notes, similar to those of Stock Dove (*Columba oenas*), at rate of 5-8 per 5 seconds; also short barking calls.

Habitat. Semi-open areas with trees and bushes, including cultivation, palm groves, orchards, riverine woodland; also parks, large gardens in towns; generally in more arid areas than *O. scops*, and in Pakistan in semi-desert and stony foothills, rocky gorges and similar arid habitats; on migration and in winter, also in acacias in desert. Mostly lowlands, but to 1800 m in Pakistan; tends to avoid mountains in WC Asia.

Food and Feeding. Insects, such as beetles, moths, locusts and mole-cricket (Gryllotalpidae), and spiders; also small mammals (rodents, shrews, bats), birds (especially small passerines), lizards; prey choice probably dependent on availability. Hunts from perch, dropping down to take prey from branch or ground; also pursues and catches aerial prey, such as moths and bats, on the wing. Sometimes forages in morning or afternoon.

Breeding. Pairing begins on arrival in N parts of range, usually Mar; lays Apr-May in most of range, to Jun in Uzbekistan. Very vocal during breeding season. Nest 3-6.5 m above ground in hollow tree, particularly poplar (*Populus*), willow (*Salix*) or mulberry (*Morus*), in old woodpecker hole, or in cavity in bank, wall, cliff or building; also in nestbox; often uses Magpie (*Pica pica*) nests locally, e.g. in Uzbekistan, 4-6 eggs; incubation 26-28 days; hatching asynchronous, chick with white down; fledging period 28-30 days. In Uzbekistan, from 18 eggs in 4 nests, 6 young fledged.

Movements. Resident and migratory. Apparently resident in Iran, and thought primarily resident in Pakistan. Extent of movements uncertain in some areas, e.g. possibly only summer visitor in Turkey; probably partial migrant in Iraq, normally encountered Mar-Oct only. Migratory in NE of range, arriving late Mar or Apr and leaving Sept/Oct; recorded in China Apr-Oct. Scarce migrant and winter visitor in S Israel; rare visitor in India.

Status and Conservation. Not globally threatened. CITES II. Status not well known. Common in Iraq; scarce in Pakistan. Recorded densities in NE of range low, e.g. from 2 pairs/2.5 km² to 10-12 pairs/400 km². May be reasonably common in much of range, but few data. No known threats.

Bibliography. Ali & Ripley (1981), Aspinall (1996), Beaman (1994), Beaman & Madge (1998), van den Berg *et al.* (1988), Cramp (1985), Etchécopar & Hùe (1964, 1978), Evans (1994), Flint *et al.* (1984), Fry *et al.* (1988), Goodman *et al.* (1989), Grimmett *et al.* (1998), Hùe & Etchécopar (1970), Jennings (1995), Kemp & Kemp (1998), Knystautas (1993), Mendelsohn (1996), Mikko (1983), Mukherjee (1995), Paz (1987), Porter, Christensen & Schiermacker-Hansen (1996), Ripley (1982), Roberts (1991), Roberts & King (1986), Shinhai (1993, 1996), Snow & Perrins (1998), Stepanyan (1990), Voous (1988), Zhao Zhengjie (1995).

22. African Scops-owl

Otus senegalensis

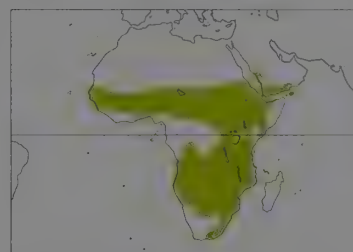
French: Petit-duc africain **German:** Afrika-Zwergohreule **Spanish:** Autillo Africano

Taxonomy. *Scops Senegalensis* Swainson, 1837, Gambia. Probably forms superspecies with *O. brucei*, *O. scops*, *O. sunia* and *O. flammeolus*. Formerly considered conspecific with *O. scops*, but separated specifically on basis of differences in voice, plumage and size. Races *socotranus* and *pamelae* sometimes placed with *O. brucei*, but closer to present species, or may even be specifically distinct. Several additional races described on basis of differences in plumage, morphology and/or size: populations from C Ethiopia to Somalia and N Kenya, from NE Zaire and W Uganda, and from Swaziland and E Cape Province sometimes separated as, respectively, *caecus*, *ugandae* and *latipennis*, but probably only colour morphs; birds described

from S Sudan and NW Ethiopia (*pygmaea*), E Kenya and Tanzania (*graueri*), Angola E to Malawi (*hendersonii*), E Malawi to N Mozambique (*pasilus*) and Namibia to N Natal and S Mozambique (*intermedius*) poorly differentiated and seem to fall within range of variation of nominate. Five subspecies currently recognized.

Subspecies and Distribution.

O. s. senegalensis (Swainson, 1837) - from Senegal and Sierra Leone E to NW Ethiopia and Somalia, S (except in SE Kenya) to SE South Africa.
O. s. pamelae Bates, 1937 - S Saudi Arabia.
O. s. socotranus (Ogilvie-Grant & Forbes, 1899) - Socotra I.
O. s. feae (Salvadori, 1903) - Annobon I (Pagalu), in S Gulf of Guinea.
O. s. nivosus Keith & Twomey, 1968 - SE Kenya (lower Tana R to Lali Hills).



Descriptive notes. 16-19 cm; wingspan c. 40-45 cm; 45-123 g. Occurs in grey-brown and rufous-brown morphs. Greyish facial disc bordered by black, with short white eyebrows and white-edged ear-tufts; dark grey-brown or rufous-brown above, streaked and mottled with black, streaks broader on crown; often rufous-buff on neck and wing-coverts; scapulars boldly white-spotted; flight-feathers and tail well barred; underparts finely vermiculated with narrow dark shaft streaks; iris yellow; bill dark horn; feet greyish. Juvenile similar to adult, but washed with brown. Races well differentiated: *feae* much darker, with rusty feather edges.

streaks broad and heavy; *socotranus* pale grey-brown, poorly marked above; *pamelae* pale brownish-grey and whitish, often rufous tinge on wing-coverts, broader white eyebrows; *nivosus* paler still, grey and white, with lower underparts plain white. Voice. Short purring, frog-like trill, "krrrup", repeated at intervals of 5-10 seconds for long periods; female slightly higher-pitched. Socotran birds said to utter quiet introductory "woup-woup".

Habitat. Wooded savanna, dry, open woodland, forest clearings, park-like habitats, bushveld, and acacia scrub; also large gardens with tall trees, and in W Africa occasionally mangroves. Roosts during day in dense foliage and alongside open trunks and branches, using favoured sites for weeks on end. From sea-level to 2000 m.

Food and Feeding. Mostly insects, including beetles, mantids, crickets and grasshoppers, and cockroaches, and spiders and scorpions; prey delivered to nest also include small vertebrates, with small numbers of geckos and lizards, frogs, and more rarely small mammals and birds (small passerines). Dietary habits similar to those of *O. scops*. Hunts by dropping on to prey from perch. Occasionally hunts on foot; also observed foraging along dead tree trunk and pulling at bark to capture a moth and woodlouse, and foraging along rocks in dry river to capture a millipede. Most prey caught on ground, but insects often seized in flight. Probably hunts within 500 m of nest. Strictly nocturnal.

Breeding. Lays generally at start of rains: Feb-Mar and Sept in W Africa, Apr-May in Sudan, Aug-Dec in E Africa, mainly Aug-Nov (peak Oct) in S Africa. Monogamous. Solitary, but occasionally pairs in close proximity, still territorial. Nest in small cavity in tree, including old woodpecker hole, or in broken tree top, up to 10 m above ground; in Namibia, once in side of old stick nest of Lappet-faced Vulture (*Torgos tracheliotus*). 2-4 eggs, usually 3; incubation 20-24 days; chick with whitish-grey down; young brooded until c. 12 days, leave cavity at c. 26 days.

Movements. Little information. Some evidence that birds from S of Limpopo R may move N into Zimbabwe in winter.

Status and Conservation. Not globally threatened. CITES II. Generally common throughout range, and locally very common, especially in wooded savanna, where up to 12 individuals heard from single spot. Widespread in S Africa; considered rare in E Cape. Occurs in a considerable number of protected areas in most countries throughout its extensive range. Secretive habits make any accurate assessment of numbers difficult.

Bibliography. Ash & Miskell (1998), Bannerman (1953), Barlow *et al.* (1997), Beaman (1994), Benson & Benson (1977), Benson *et al.* (1971), Brown *et al.* (1987), Cave & Macdonald (1955), Cheke & Walsh (1996), Dixon (1994), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Elglood *et al.* (1994), Field (1998), Friedmann (1930), Fry *et al.* (1988), Gallagher (1986), Gatter (1997), Ginn *et al.* (1989), Giraudoux *et al.* (1988), Gore (1990), Grimes (1987), Harrison *et al.* (1997), Jennings (1995), Keith & Twomey (1968), Kemp & Calburn (1987), Kemp & Kemp (1998), Lewis & Pomeroy (1989), Mackworth-Prace & Grant (1957, 1962, 1970), Maclean (1993), Madge (1972), Marshall (1978), Mitchell (1992), Morel & Chappuis (1992), de Naurois (1994b), Penry (1994), Pickford *et al.* (1989), Pinto (1983), Porter, Christensen & Schiermacker-Hansen (1996), Rieker (1986), Ripley & Bond (1966), Short *et al.* (1990), Snow (1978), Steyn (1982, 1984, 1994b), Vernon (1991b), van der Weyden (1973), Zimmerman, D.A. *et al.* (1996).

23. Eurasian Scops-owl

Otus scops

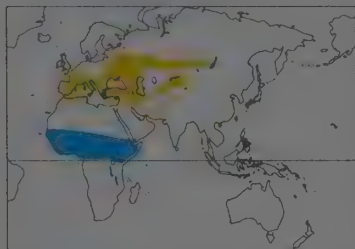
French: Petit-duc scops **German:** Zwergohreule **Spanish:** Autillo Europeo
Other common names: European/Common Scops-owl

Taxonomy. *Strix Scops* Linnaeus, 1758, Italy. Probably forms superspecies with *O. brucei*, *O. senegalensis*, *O. sunia* and *O. flammeolus*. Formerly considered to include *O. mirus*, *O. longicornis*, *O. mindorensis*, *O. brucei*, *O. senegalensis*, *O. sunia*, *O. mantananensis*, *O. elegans*, *O. umbra*, *O. enganensis* and even *O. hartlaubii*, all now shown to be separated specifically by voice and, in some cases by DNA. Six subspecies recognized.

Subspecies and Distribution.

O. s. scops (Linnaeus, 1758) - France, Italy and C Mediterranean islands E to Volga R, S to N Greece, N Turkey and Transcaucasia; intergrades with *pulchellus*.
O. s. pulchellus (Pallas, 1771) - Volga R E to L Baikal, S to Altai and Tien Shan.
O. s. mallorcae von Jordans, 1923 - Iberia, Balearic Is, NW Africa (NC Morocco to Tunisia).
O. s. cycladum (Tschusi, 1904) - S Greece and S Asia Minor, S to C Israel and Jordan.
O. s. cypricus (Madarász, 1901) - Cyprus.
O. s. turanicus (Loudon, 1905) - Iraq and Iran (and perhaps this race SE Turkey) E to NW Pakistan.

Descriptive notes. 16-20 cm; wingspan 53-64 cm; 60-135 g. Occurs in grey-brown and rufous-brown morphs, latter less frequent. Facial disc grey, darker grey-brown around eyes; with thin whitish eyebrows; crown, small ear-tufts and upperparts brown-grey to rufous-brown with blackish-brown streaks, bars and vermiculations, nape with pale spots, mantle sides more rufous; line of black-tipped white or pale buff spots along scapulars; outer primaries broadly barred buff-white, tail more



narrowly barred; underparts lighter brown to buffish-white with black-brown streaks, thin bars and vermiculations, streaks widest on flanks; iris yellow; bill blue-black; legs noticeably thin, feathered buff-white; feet grey. At close range, differs from *O. brucei* in generally darker and more heavily marked appearance, pale nape spots, dark cross-bars below and presence of pale horizontal panels on belly; at distance confusable with *Athene noctua*, but has more upright stance, longer silhouette, lacks obvious pale spots above, is less boldly streaked below. Juvenile with less conspicuous streaks and vermiculations, especially on

underparts. Races vary in ground colour of plumage and in strength of dark markings: *pulchellus* mostly somewhat paler than nominate, with slightly narrower markings, and pale nape spots larger and more extensive; *malloreae* smaller, markings heavier; *cycladum* with darker and coarser markings; *cyprius* darkest race, dark grey-brown, with markings dark and coarse, white spots more distinct; *iranicus* pale silvery-grey, with dark shaft streaks narrow and sharply defined. Voice. Male territorial call a low, short whistle, "tyeu", repeated at intervals of 2-3 seconds for long periods; female higher-pitched; frequent duets during courtship.

Habitat. Breeds in rather open and semi-open broadleaved woodland, including parks, orchards and plantations, also cultivation with groves, and large gardens, riverine forest, roadside trees, and trees in quiet squares in small towns; locally, e.g. in Russia, mixed and open coniferous forest, and juniper (*Juniperus*) woodland; in Pakistan, juniper scrub and holly oak (*Quercus ilex*) in dry, rocky country; in general, requires good cover of trees, with suitable sites for roosting and nesting, and adjacent open ground with plenty of large insect prey; avoids closed forest and extensive open areas. In African winter quarters, prefers wooded savanna and tall grass with dense bushes, bushy country, acacias in dry river beds; in Senegal, found in dense bamboo. Breeds from sea-level to c. 2000 m; in Pakistan, locally to 3000 m.

Food and Feeding. Mostly insects and other invertebrates; also earthworms, spiders, and some small birds, reptiles, amphibians and mammals. Insects mostly crickets and grasshoppers (Orthoptera), beetles and moths; other prey include crustaceans (amphipods, isopods), tree frogs (*Hyla*), birds to size of Redwing (*Turdus iliacus*), and mice; bats and shrews taken occasionally. In S Spain, 159 items comprised 94.3% invertebrates, 2.5% reptiles, 1.2% amphibians, 1.2% mice and 0.6% birds. Hunts from perch, flying down to grab prey with feet, or may initially land alongside; also hunts on foot, seizing small prey with bill; pulls earthworms from ground with bill; moths caught in feet after fast aerial pursuit. Small insects swallowed whole; larger ones, and vertebrates, pulled apart; birds plucked. Nocturnal, occasionally diurnal.

Breeding. Season Mar-Aug in S Europe; lays May-Jun in N Africa. Monogamous, occasionally polygynous. Solitary; few records of pairs nesting in loose groups. Nest in tree cavity, hole in building or wall, or occasionally old nest of other species, especially Magpie (*Pica pica*) or raptor, sometimes disused burrow of bee-eater (*Merops*); readily accepts nestboxes; same site sometimes used for several years, though not known if by same pair; in 2 successive years, pair used sites 350 m apart. 2-6 eggs, normally 3-4; replacement clutch laid if first lost; laying interval 1-3 days; incubation generally 24-25 (20-31) days, by female, from second, third or last egg; hatching asynchronous, 4-5 young over 3 days; chick with white to pale grey down; female performs almost all brooding; young leave nest at 21-29 days, able to fly well by 30-33 days, cared for by parents for c. 5 weeks. Age of first breeding in wild unknown, probably 1 year. Oldest ringed bird 6 years.

Movements. Mostly migratory; S populations either partially so or resident. Wholly resident in Cyprus; *malloreae* present all year in Balearics and S & E Spain, although winter numbers considerably reduced, emigrants presumably making short-distance migrations to Africa, where several trapped in N during passage periods; *cycladum* largely migratory, some birds winter in S Italy and S Greece; Pakistan breeders winter largely in S Pakistan, some probably in W India. Remaining populations apparently all long-distance migrants, leaving breeding grounds from Aug onwards; most reach Afrotropical savanna regions in winter; return migration from late Mar. Overshooting migrants in spring occasionally reach N & NW Europe. Family may stay together during migration.

Status and Conservation. Not globally threatened. CITES II. In mid 1990's, European population estimated at 77,000-96,000 pairs, plus possibly 50,000 pairs in European Russia and 30,000 pairs in Turkey; main strongholds in Spain and Croatia, with c. 32,000 and 21,000, respectively; numbers generally stable or decreased; decline of over 50% in Austria, Switzerland and Ukraine; some increase in Hungary. Considered not rare in suitable habitat in Russia; in Lebanon, abundant in Bekaa valley (1974); marked population decrease in Israel due to pesticide use, but some recovery since 1970's; common in Cyprus. Marked range contraction in Europe in 20th century probably due to habitat changes and reduction in insect populations; in France, contracted towards S, since 1936 extinct in several areas in N half of country and only accidental in others, possibly related to decrease in populations of large insects due to widespread large-scale farming, or reduction in number of hollow trees; extinct in many former breeding areas in Switzerland, where habitat fragmented by spread of viticulture and agricultural intensification; similar history in Austria, where decreased from c. 50-150 pairs in 1983 to 20-30 in mid 1990's.

Bibliography. Ali & Ripley (1981), Arlettaz (1987, 1988, 1989, 1990a), Arlettaz & Fournier (1991, 1993), Bavoux & Burneleu (1985, 1991), Bavoux, Burneleu, Juillard & Nicolau (1993), Bavoux, Burneleu & Nicolau (1991), Beaman & Madge (1998), Colston & Curry-Lindahl (1986), Cottier & Maumary (1993), Cramp (1985), Danko & Paenovsky (1995), Díaz, Asensio & Tellería (1996), Dowsett & Dowsett-Lemaire (1993), Échécopar & Hùe (1964, 1978), Evans (1994), Fajardo & Babiloni (1996a, 1996b), Flint *et al.* (1984), Friedmann (1930), Friedmann & Keith (1968), Fry *et al.* (1988), Galeotti & Garibaldi (1994), Galeotti, Sacchi & Perani (1997), Gatter (1997), Goodman *et al.* (1989), Gorman (1995), Gragera (1996), Grimmett *et al.* (1998), Hagemeijer & Blair (1997), Handrinos & Akriotis (1997), Heller & Heller (1979, 1984), Henninger & Benderet (1990), Hùe & Échécopar (1970), Kämpfer-Lauenstein *et al.* (1993), Kemp & Kemp (1998), Kempf (1972), König (1973), Kumerloewe (1962), Landmann (1978), Le Gassic (1993), Ledant *et al.* (1981), MacKrell (1986), MacKworth-Pried & Grant (1957, 1970), Máñez (1994a), Marshall (1978), Martínez, J.A., Izquierdo *et al.* (1996), Meier-Zwicky (1993), Mendelssohn (1996), Mikkola (1983), Murray & Chappuis (1992), Mukherjee (1995), Paz (1987), Porter, Christensen & Schiermacker-Hansen (1996), Porro (1997), Ripley (1982), Roberts (1991), Roberts & King (1986), Rogacheva (1992), Rogier (1971), Rutgers & Norris (1972), Samwald & Samwald (1992), Shirihai (1993, 1996), Simeonov *et al.* (1990), Snow & Perrins (1998), Sorace (1991), Stepanyan (1990, 1995), Strel & Kalotas (1987, 1991), Vidal *et al.* (1984), Voous (1984, 1988), van der Weyden (1973, 1975), Zhao Zhengjie (1995), Zimmermann, D.A. *et al.* (1996).

24. Oriental Scops-owl

Otus sunia

French: Petit-due d'Orient **German:** Orient-Zwergohreule **Spanish:** Autillo Oriental
Other common names: Asian/Indian(?) Little/Eastern Scops-owl, East Asian Screech-owl

Taxonomy. *Scops sunia*, Hodgson, 1836, Nepal.

Probably forms superspecies with *O. brucei*, *O. senegalensis*, *O. scops* and *O. flammeolus*. Sometimes treated as conspecific with *O. scops*, and has been considered conspecific both with *O. senegalensis* and with *O. brucei*, or to include *O. mirus*, *O. mindorensis*, *O. mantananensis*, *O. elegans*, *O. umbra* and *O. enganensis* as races; all now shown to be specifically distinct on basis mainly of vocalizations. Proposed races *nicobaricus* and *distans* (Thailand) synonymous with *modestus*, although *nicobaricus* may prove to be a valid taxon; according to some, even *modestus* itself is possibly inseparable from *malayanus*. Original specimen of *O. alius* initially assigned to race *nicobaricus* (= *modestus*) of present species. Seven subspecies recognized.

Subspecies and Distribution.

O. s. sunia (Hodgson, 1836) - N Pakistan E to Bangladesh, and N India.

O. s. rufipennis (Sharpe, 1875) - S India.

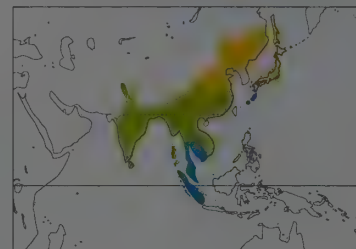
O. s. leggei Ticehurst, 1923 - Sri Lanka.

O. s. modestus (Walden, 1874) - Assam (S to Brahmaputra R), Myanmar, N & W Thailand, Indochina; also Andamans and C Nicobars (Camorta).

O. s. malayanus (Hay, 1847) - S China (Yunnan E to Guangdong).

O. s. stictonotus (Sharpe, 1875) - SE Siberia, Sakhalin, NE China, N Korea.

O. s. japonicus Temminck & Schlegel, 1844 - Japan.



Descriptive notes. 18-21 cm; wingspan 50.5-52.6 cm; 75-95 g. Occurs in grey-brown and rufous morphs. Grey-brown morph similar to corresponding plumage of *O. scops*, differing mainly in less patterned upperparts and stronger black streaking below, but variable; rufous morph plain rufous above, apart from white scapular line and finely dark-streaked forehead and crown, and lighter below, breast with dark shaft streaks and thin horizontal pencil-lines; eyes yellow; bill horn-green or horn-yellow, tipped blackish; feet yellowish-grey or greyish-flesh colour. Differs from *O. bakka-moena* in lack of prominent nuchal collar. Ju-

venile as adult but with faint barring. Races *stictonotus* and *japonicus* larger and paler than nominate; *malayanus* and *rufipennis* dark; *leggei* darkest and smallest. Voice. Utters 3 "toik" calls in rhythmic phase, repeated at regular short intervals; in Thailand and Sri Lanka 4-note "toik" reported, with rhythm resembling that of "Here comes the bride".

Habitat. Prefers deciduous and mixed forest but not uncommon in open evergreen forest, and found also in riparian woodland, orchards and parkland; in Indian Subcontinent also groves in and around settlements and cultivation, and said to occur around city street lights in Sri Lanka; in Japan seems to prefer taller trees, and often found around temples; also gardens in winter in S. Mainly lowlands and foothills, to 1500 m, but up to 2300 in Himalayas.

Food and Feeding. Primarily insects and spiders; also small rodents and small birds. Prefers to feed along edges, in open, park-like woods, or in glades; forages both from the forest floor and in the canopy. Hunts from perch, dropping down on to prey, but frequently also in flight.

Breeding. Lays mid Feb-Apr/May in India and Pakistan, Apr-Jun in Siberia and China, May-Jun in Japan. Nest a hollow in a tree trunk, a nestbox, or a hole in a wall, at very variable height above ground. 3-6 eggs, usually 3-4; incubation 24-25 days; chick with whitish down.

Movements. N populations largely migratory, S ones resident. Birds from Siberia to N China and Japan winter mostly from S China to Thailand and S to Malaysia, and Sumatra (2 records, Jan and Mar); in Japan present mostly May-Sept/Oct, with very few noted in C & S parts in winter; some short-distance movements recorded in Himalayan region.

Status and Conservation. Not globally threatened. CITES II. Varies in abundance regionally; scarce and very local in Pakistan, and scarce but more widespread in Sri Lanka, but fairly common in most of Indian Subcontinent; uncommon in Thailand; uncommon in Japan, but said to be commonest strigid in SE Siberia.

Bibliography. Ali & Ripley (1981), Armstrong (1983), Beaman (1994), Brazil (1991), Brazil & Yamamoto (1989a), Deignan (1945), Flint *et al.* (1984), Grimmett *et al.* (1998), Inskipp, C. & Inskipp (1991), Inskipp, T. *et al.* (1996), Knystautas (1993), Lekagul & Round (1991), van Marle & Voous (1988), Marshall (1978), Medway & Wells (1976), Phillips (1978), Phillips & Henry (1933), Riley (1938), Ripley (1982), Roberts (1991), Roberts & King (1986), Sankaran (1998), Smythies (1986), Sora *et al.* (1996), Stepanyan (1990, 1995), Tikader (1984), Voous (1988), Wells (1999).

25. Flammulated Owl

Otus flammeolus

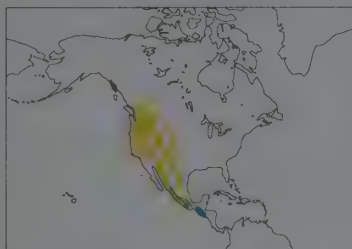
French: Petit-due nain **German:** Ponderosaeule **Spanish:** Autillo Flamulado
Other common names: Flammulated Screech-owl

Taxonomy. *Scops (Megascops) flammeola* Kaup, 1853, Mexico.

Only New World species belonging to the Old World *Otus* assemblage referred to as subgenus *Otus*; differs from other New World *Otus* (subgenus *Megascops*) in lacking typical trilled song. Probably forms superspecies with *O. brucei*, *O. senegalensis*, *O. scops* and *O. sunia*. Longer-winged population in N part of range sometimes separated as *idahoensis* and darker birds from Guatemalan highlands described as *rufus*, but individual plumage variation appears to be continuous and biometric differences possibly clinal; also, other races described from S Mexico and Guatemala (*meridionalis*), Colorado (*frontalis*) and C British Columbia to NE California (*borealis*); type locality of species, however, apparently unknown, making objective use of subspecific names problematic. Treated as monotypic.

Distribution. Breeds from SW Canada (SC British Columbia) S to NW & SW USA and NE, W & C Mexico (and E in highlands to S Puebla, and NE Oaxaca). Winters to C & S Mexico and Guatemala, possibly El Salvador.

Descriptive notes. 15-17 cm; 45-63 g. Occurs in grey-brown and rufous morphs, with many intermediates and much individual variation; generally greyer in N and more rufous in S, with short, flattened ear-tufts. Facial disc pale greyish, with variable rufous wash strongest around eyes, faint darker concentric rings, and short white eyebrows; disc bounded by black-spotted dark rufous to solid black, and edged with buff; rest of plumage with black shaft streaks, cross-lines, and varying degree of rufous wash, scapulars with rufous-tinged creamy spots forming bold stripe; flight-feathers and tail with lighter bands; belly whitish with dark streaks and vermiculations; iris dark brown; bill grey-brown; tarsi densely feathered grey-brown to base of toes. Distinguished from other American *Otus* by size and short ear-tufts. Juvenile barred grey on white to pale greyish ground colour, but without longitudinal streaks of subsequent plumages. Voice. Rather deep, hollow, short "hoop", singly or repeated at intervals of 2-3 seconds; also double "hoo-hoop" notes in excitement.



Habitat. Primarily open coniferous forest in mountains, especially ponderosa pine (*Pinus ponderosa*) forest, or similar habitat, e.g. dry montane conifer forest mixed with aspen (*Populus*) or oak (*Quercus*), generally with brushy understorey. Nests in or near open conifer forest with large old trees, scattered thickets of saplings and/or shrubs, and clearings; in British Columbia, avoids pure ponderosa pine forest, opting for dry interior Douglas fir stands with open aspect, including selectively logged areas. Common features of habitat N of Mexico include cool, semi-arid climate, high abundance of nocturnal arthropod prey and some

dense foliage (preferred roosting habitat); in W North America restricted to mid-elevation montane zone, not extending to coastal pine belt or easternmost yellow pines; upper elevational limit perhaps set by low nocturnal temperatures, lower by high daytime temperatures or humidity. In Mexico, found at 1500–3000 m.

Food and Feeding. Almost entirely nocturnal insects, especially owl moths (Noctuidae), beetles, and crickets and grasshoppers; in observation in Colorado, owl moths appeared to be only food available during cold spring nights. Also spiders, and some small mammals, e.g. a shrew (*Sorex*) removed from stomach of apparently healthy owl that struck window; perhaps also a few small birds. In Colorado study, forest edge the most preferred foraging area. Frequently changes perch; locates prey from perch visually, apparently by moving head vertically and horizontally, then captures it from foliage of canopy, gleams from needles or branches while hovering, or picks up prey from ground; often pursues moths in air, seizing them with bill, and returns to same or different perch. Captive fledglings used feet to capture prey, including moths taken in upside-down position from ceiling. Nocturnal, with crepuscular foraging peaks during breeding.

Breeding. Season May–Aug. Monogamous, but extra-pair copulations occur; no divorce in 5 cases when both members of pair returned in subsequent year; when mates failed to return, females tended to move to adjacent territory and pair with widowed male; widowed males do not move. Solitary, but sometimes several pairs in close proximity to one another, territories possibly overlapping. Nest in natural cavity, old woodpecker hole, or nestbox. 2–4 eggs; replacement clutches rare; incubation 21–24 days, by female, fed at nest by male but still loses weight; chicks hatch with eyes closed, covered with white down; fledging c. 25 days; fledglings remain within 100 m of nest for 1 week after fledging, fed every 1–5 minutes by parents, then move away, passing through adjacent home ranges; in second week attempt to glean insects and follow adults on feeding trips, but sporadic feeding by parents continues; independent after c. 5 weeks. Fledging rates in successful nests 83% in New Mexico and 100% in Colorado, with total nest failure rate 18% and 13%, respectively, yielding probability of fledging 0.67 and 0.74; production per nest 1.5 for New Mexico and 2.3 for Colorado, and mean of 2.7 fledglings for 9 successful nests in Oregon. Age at first breeding unknown. Maximum recorded age in wild 8 years 1 month; lifespan probably much longer.

Movements. Still poorly understood. Altitudinal and translatitudinal migration hypothesized for N populations S to N Mexico, and very probable that many N birds winter in area from C Mexico to Guatemala, or extending to El Salvador (several winter records); S Mexican populations more likely resident. High breeding-site fidelity and variation of diet with prey abundance make nomadic behaviour unlikely. Vagrants recorded in USA E to Florida.

Status and Conservation. Not globally threatened. CITES II. Common in North America, but considered sensitive in USA and vulnerable in Canada; in Mexico fairly common to common, but local. Greatest intrinsic source of danger may be low reproductive rate. Potential threats include pesticides, pollution, and habitat change or destruction. Forest change and insecticide use could influence insect populations on which species depends; most visible impact is loss of nest cavities, and healthy woodpecker populations therefore important; occasionally uses nestboxes, although may be sensitive to type and/or placement, and further study needed. If requirement for old-growth timber verified, intensive management could be needed; silviculture not necessarily incompatible, as some aspects (controlled burning, thinning) tend to open up forest, but availability of nest-sites, roost-sites and adequate foraging areas important.

Bibliography. Atkinson & Atkinson (1990), Baicich & Harrison (1997), Balda *et al.* (1975), Bloom (1983), Bull & Anderson (1978), Bull *et al.* (1990), Burt *et al.* (1987), Campbell *et al.* (1990), Cannings, R.A. (1974), Cannings, R.J. (1994), Cannings, R.J. & Cannings (1982), Cannings, R.J. *et al.* (1978), Collins *et al.* (1986), Contreras-Balderas (1992), DeGraaf & Rappole (1995), Dunham & Butcher (1996), Eckert (1974), Fix (1987), Goggans (1986), Groves & Frederick (1997), Hasenyager *et al.* (1979), Hayward (1983, 1986), Hayward & Verner (1994), Heintzelman (1992), Holt (1996), Holt & Hillis (1987), Holt *et al.* (1987), Howell & Webb (1995a), Howie & Ritcey (1987), Johnsgard (1988), Kaufman (1996), Linkhart (1986), Linkhart & Reynolds (1987, 1994), Marcot & Hill (1980), Marshall, J.T. (1978, 1997), Marti (1986), McCallum (1994, 1996), McCallum & Gehlbach (1988), McCallum *et al.* (1995), Phillips (1942), Powers *et al.* (1996), Reynolds (1987), Reynolds & Linkhart (1987a, 1987b, 1987c, 1990a, 1990b), Richmond *et al.* (1980), Ross (1969), Small (1994), Smith (1991), Stotz *et al.* (1996), Tyler & Phillips (1978), Urban (1959), Voous (1988), Walker (1993), Webb (1982b), Winter (1974), Wolfe & de la Torre (1990).

26. Moluccan Scops-owl

Otus magicus

French: Petit-duc mystérieux **German:** Molukken-Zwergohreule **Spanish:** Autillo Moluqueño
Other common names: Mysterious/Insular Scops-owl

Taxonomy. *Strix magica* S. Müller, 1841, Ambon (South Moluccas).

Probably forms superspecies with *O. mantananensis*, the two being closely allied to the *O. manadensis* superspecies. Sometimes considered conspecific with *O. manadensis*, or variously to include *O. beccarii*, *O. enganensis* and *O. insularis* as races, but all shown to be morphologically and/or vocally distinct; moreover, *O. alfredi* recently treated as a rufous morph of race *albiventris* of present species, but shown by morphological study to be distinct and separate species. Classification and true affinities of *Otus* taxa in SE Asia, particularly island forms, highly complex and still debatable, and relationship between present species and *O. manadensis* confused: forms *siaensis*, *mendeni*, *kalidupae* and *sulaensis* currently included in latter, but some or all sometimes placed with present species; current arrangement highly tentative, and further research required. Also, described races *leucospilus* and *obira* have been thought possibly synonyms of nominate race of present species, though at least the former distinct enough. Seven subspecies currently recognized.

Subspecies and Distribution

O. m. morotensis (Sharpe, 1875) - Morotai, Ternate.
O. m. leucospilus (G. R. Gray, 1860) - Halmahera, Kasiruta, Bacan.
O. m. obira Jany, 1955 - Obi Is.

O. m. magicus (S. Müller, 1841) - Seram, Ambon.
O. m. bouruensis (Sharpe, 1875) - Buru.
O. m. albiventris (Sharpe, 1875) - Lombok, Sumbawa, Flores, Lombok.
O. m. tempestatis (Hartert, 1904) - Wetar.



Descriptive notes. c. 25 cm; 114–165 g. Occurs in grey-brown, rufous and yellow-brown morphs, with various intermediates. Facial disc whitish with variable rufous to greyish tinge, and short white eyebrows; crown dark-streaked, ear-tufts barred; upperparts variably streaked and barred dark, bars sometimes strong, and scapulars with dark-tipped white spots which can be indistinct; flight-feathers prominently barred whitish, tail with thinner pale bars; underparts much paler than upperparts, usually coarsely streaked and with broken thin cross-lines; iris yellow; bill light yellowish-grey; distal 7–9 mm of tarsus

unfeathered, yellowish to greyish. All races of present species differ from *O. manadensis* mainly in more heavily barred tertials and uppertail. Juvenile has barred rather than streaked crown. Races variable, differ in size and general plumage coloration: *bouruensis* rather uniform buffy-brown above and white below; *tempestatis* and *albiventris* small, former with nearly fully feathered tarsus, latter with whiter and much less patterned lower underparts. **Voice.** Male territorial call a harsh, barking, raven-like croak, repeated at intervals of a few seconds, sometimes even harsher and more rapidly repeated; female slightly higher-pitched.

Habitat. Observed primarily in forested areas, and often in coastal swamp-forest; also secondary growth, well-forested limestone cliffs, locally large trees in settlements, palm plantations. Lowland and coastal areas, commonly up to 900 m, locally to 1500 m.

Food and Feeding. Insects; probably a few small vertebrates taken on occasion.

Breeding. Nestlings noted in Nov and Dec; nest probably in tree cavity; no other information.

Movements. Presumably resident.

Status and Conservation. Not globally threatened. CITES II. Considered common on Buru and uncommon on Sumbawa; no data on status from rest of range. Occurs in Manusela National Park, Seram, and Kali Batu Putih, Halmahera. Forest destruction probably a threat in the long term.

Bibliography. Andrew (1992), van Bemmel (1948), Bowler & Taylor (1989), Coates & Bishop (1997), Indrawan *et al.* (1997), Inskipp *et al.* (1996), Isherwood *et al.* (1997), Johnstone *et al.* (1996), Marshall (1978), Ripley (1959), Siebers (1930), White & Bruce (1986).

27. Mantanani Scops-owl

Otus mantananensis

French: Petit-duc de Mantanani **German:** Philippinen-Zwergohreule **Spanish:** Autillo de la Mantanani
Other common names: South Philippines Scops-owl

Taxonomy. *Scops mantananensis* Sharpe, 1892, Mantanani Island.

Probably forms superspecies with *O. magicus*, the two being closely allied to the *O. manadensis* superspecies. Previously treated as conspecific with *O. scopis* or *O. sunia*, but vocally distinct from both. Island population off N Luzon (*calayensis*), included with *O. elegans*, sometimes placed with present species. Sulu form *sibutuensis* has been considered race of *O. manadensis*. Tumindao population (*steerei*) regarded as inseparable from *sibutuensis*. Racial allocation highly tentative, however, as no specimens known for many of islands listed. Four subspecies recognized.

Subspecies and Distribution.

O. m. romblonis McGregor, 1905 - Banton, Sibuyan, Romblon, Tablas, Tres Reyes and Semirara, in C Philippines.

O. m. cuyensis McGregor, 1904 - S Calamian Is (Dicabaito, Linapacan) and Cuyo I.

O. m. mantananensis (Sharpe, 1892) - Mantanani I, off N Borneo, and islands off S coast of Palawan.

O. m. sibutuensis (Sharpe, 1893) - Sibutu and Tumindao, in SW Sulu Is.



Descriptive notes. 18–20 cm; c. 100–110 g. Occurs in brownish and rufous morphs. Facial disc pale buffish with distinct thin dark border, and narrow whitish eyebrows; crown and short ear-tufts spotted dark, hindneck with black triangular spots; upperparts generally dark brown, mottled with black, with complex shaft streaks; outer webs of scapulars whitish; flight-feathers and tail barred pale; underparts much paler (perhaps even whitish) and peppered with black streaks and broken cross-lines, breast with variable rufous tinge; iris yellow; feet and bill grey; tarsus almost fully feathered. Juvenile of nominate race not described; *sibutuensis* whitish,

heavily barred dark brown, crown and breast plainer brown, more prominent barring on tertials and tail. Races differ in plumage tone, paler, more grey or more rufous: *romblonis* with general rufous tinge, nearly unbarred tertials and uppertail, heavily marked below; *sibutuensis* usually dull brown with irregular, subdued markings, reduced pale colour on scapulars; *cuyensis* large, with conspicuous black streaking. **Voice.** Male generally a deep, nasal, goose-like honk, repeated at intervals of c. 5–6 seconds; this often followed by 3–6 or more lower-pitched gruff notes, possibly from duetting female (though female *Otus* usually have slightly higher voice).

Habitat. Forest, woodland, coconut groves and casuarina trees; hunts at edges of wood, in clearings and among secondary growth. Lowlands and foothills.

Food and Feeding. Apparently mostly insects.

Breeding. Possibly lays Mar–May; nest in tree cavity; no other information.

Movement. Resident throughout range.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Sulu Archipelago EBA and Palawan EBA. Noted as common on Mantanani I in forest and coconut plantations; no data from elsewhere. Destruction of forest could be long-term threat, but some reports that species generally found away from tracts of undisturbed forest, and also near farmland areas, may indicate ability of at least some races to tolerate man-altered habitats.

Bibliography. Alcala & Alviola (1970), Baud (1976), Dickinson *et al.* (1991), Goodman *et al.* (1995), Inskipp *et al.* (1996), MacKinnon & Phillips (1993), Manuel (1956), Marshall (1978), McGregor (1909–1910), Mearns (1909a), Oliver & Wirth (1996), Stattersfield *et al.* (1998).

ssp elegans

28

ssp calayensis

29

brown morph

rufous morph

30

31

dark rufous-brown morph

dark brown morph

32

33

34

35

36

brown morph

rufous morph

37

38

dark morph

rufous-brown morph

brown morph

39

rufous morph

grey-brown morph

ssp rutilus

40

rufous morph

ssp mayottensis

grey-brown morph

rufous morph

PLATE 7

inches 4
cm 10

41

28. Ryukyu Scops-owl

Otus elegans

French: Petit-duc élégant **German:** Schmuckeule **Spanish:** Autillo Elegante
Other common names: Elegant Scops-owl

Taxonomy. *Ephialtes elegans* Cassin, 1852, at sea off the coast of Japan. Probably forms superspecies with *O. manadensis* and *O. collari*. Formerly treated as conspecific with *O. sunia*, and until recently considered race of *O. scops*, but separated specifically on basis of vocal characteristics and morphology (comparatively larger feet); has recently been listed it as a race of *O. manadensis*, perhaps erroneously. Batan population sometimes separated as race *batanensis*; *interpositus* merged with nominate by some authors. S race *calayensis* placed with *O. mantanensis* by some, but seems closer to present species, at least on vocal and geographical grounds. Four subspecies recognized.

Subspecies and Distribution.

O. e. elegans (Cassin, 1852) - throughout Ryukyu Is (Nansei Shoto), S Japan.
O. e. interpositus Kuroda, 1923 - Daito Is (Minami-daito-jima).
O. e. botelensis Kuroda, 1928 - Lanyu I, off SE Taiwan.
O. e. calayensis McGregor, 1904 - Batan Is, Sabtang and Calayan, off N Philippines.

Descriptive notes. c. 20 cm. Drab brown or dark reddish-brown above, pale below, with fine and intricate black patterning, and pointed wing; silvery-grey facial disc with partial dark rim, latter bordered rufous. Resembles *O. sunia*; differs in larger size, no bright rufous morph. Juvenile buffy with fine dark barring. Races poorly differentiated: *botelensis* darker and even more finely marked than Japanese birds, often occurs in dark rufescent morph; *calayensis* generally with more rufous-buff tinge, scapular spots with ochraceous colour. Voice. Male call a hoarse, cough-like noise, "uhu" or "kuru" or "u-kuruk", lower-pitched



than *O. sunia*, repeated 15-30 times per minute; female call sounds more like "nye".

Habitat. Subtropical dense evergreen forest; locally, in or near villages. From sea-level to 550 m, probably higher.

Food and Feeding. Primarily insects, including beetles, moths, crickets and grasshoppers; also spiders, and some small mammals and small birds.

Breeding. Lays Mar-Jul. Nest in tree hole, often old woodpecker cavity. Usually 2-3 eggs, but up to 5; incubation c. 30 days; young fledge at c. 1 month. Mean fledging success 0.6 young per nest.

Movements. Probably mainly resident; N populations possibly disperse S after breeding.

Status and Conservation. Not globally threatened. Restricted-range species: present in Nansei Shoto EBA. CITES II. Common in suitable habitat throughout Ryukyus, where numbers thought to be quite large; status of race *interpositus* unknown. Race *calayensis* fairly common in forest or forest edge on Batan, Calayan and Sabtang, but total range extremely small. Lanyu race *botelensis* was formerly listed as threatened, with estimated population in mid 1980's of c. 200 individuals; more recently, however, considered to number 1000 individuals, with population stable, and prospects for survival regarded as good so long as habitat protected. Studies showed that breeding may be unsuccessful in disturbed habitats, and that suburban owls may not live so long as rural ones.

Bibliography. Beaman (1994), Brazil (1991), Brazil & Yamamoto (1989a), Clark & Mikola (1989), Dickinson *et al.* (1991), Inskipp *et al.* (1996), Kabaya & Higuchi (1977), King (1978/79), Marshall (1978), Manuel & Gilliard (1952), McGregor (1909-1910), Severinghaus (1989, 1992), Stattersfield *et al.* (1998), Zhao Zhengjie (1995).

29. Sulawesi Scops-owl

Otus manadensis

French: Petit-duc de Manado **German:** Manadoeule **Spanish:** Autillo de Célebes
Other common names: Celebes Scops-owl

Taxonomy. *Scops manadensis* Quoy and Gaimard, 1830, Manado, Sulawesi.

Probably forms superspecies with *O. elegans* and *O. collari*. Formerly treated as conspecific with *O. magicus*; also sometimes as including *O. beccarii* as race. Recently listed as including *O. elegans* as race, perhaps in error. Has traditionally been considered to include birds from Sangihe I, recently described as *O. collari*. Sulu form *sibutuensis*, included with *O. mantanensis*, sometimes placed with present species. Classification and true affinities of *Otus* taxa in SE Asia, particularly island forms, highly complex, with relationship between present species and *O. magicus* not fully understood; taxonomic status of races treated under present species unclear, with some or all sometimes treated under *O. magicus*, and current arrangement tentative. In particular, *siaoensis*, with shorter wings and much shorter and more narrowly barred tail may well be specifically distinct; *sulaensis* morphologically closer to *O. magicus* and probably better placed with that species, or perhaps specifically distinct; *mendeni* and *kalidupa* little known. Pending further research, five subspecies recognized.

Subspecies and Distribution.

O. m. siaoensis (Schlegel, 1873) - Siau I, N of Sulawesi.
O. m. manadensis (Quoy & Gaimard, 1830) - Sulawesi.
O. m. mendeni Neumann, 1939 - Banggai Is (Peleng, perhaps also Labobo).
O. m. sulaensis (Hartert, 1898) - Sula Is (Taliabu, Seho, Mangole, Sanana).
O. m. kalidupa Hartert, 1903 - Tukangbesi Is (Kaledupa).

Descriptive notes. 19-23 cm; 83-93 g. Occurs in brown and rufous morphs, latter very scarce; plumage variable. Similar to *O. magicus*, but smaller than Moluccan forms of latter; differs from all races of that species in less barred tertials and tail. Juvenile as adult but more barred, especially on crown and mantle. Race *siaoensis* much smaller, with very small ear-tufts, much shorter and more narrowly barred wings and tail; *mendeni* small, tarsus half feathered at front and bare at rear, grey morph peppered above; *sulaensis* with bare lower tarsus; *kalidupa* with feathering extending on to tops of toes, pale grey-brown, more finely patterned. Voice. For nominate race, main territorial call a clear, upward-inflected, mournful "ploek", c. 0.4 seconds long, repeated at intervals of up to 6



seconds; also rapid "kik-kok-kok-kok", and "oek-oek-oek" alternating with rising whistled "oi-oi-oi". Race *sulaensis* said to be quite different; other races unknown.

Habitat. Humid forest and forest clearings and edge, in geographical areas with high mean annual temperatures and average annual rainfall. Lowlands and hills, up to c. 2500 m above sea level.

Food and Feeding. Probably mainly insects; little information available. Nocturnal.

Breeding. Almost no information; indication that breeding may begin just before start of monsoon season.

Movements. Resident in Sulawesi, and presumably elsewhere.

Status and Conservation. Not globally threatened. CITES II. Appears to be fairly common and widespread in Sulawesi, where occurs in Tangkoko Nature Reserve and in Dumoga-Bone and Lore Lindu National Parks; two recent searches for *siaoensis*, known only from the type specimen, unsuccessful, and forest on Siau almost gone; no data on other populations, but all are poorly known and unlikely to be common. Main threat probably forest destruction.

Bibliography. Andrew (1992), Catterall (1997), Coates & Bishop (1997), Coomans de Ruiter (1950), Coomans de Ruiter & Maurenbrecher (1948), Davidson & Stones (1993), Ekstron *et al.* (1998), Holmes & Phillips (1996), Indrawan *et al.* (1997), Marshall (1978), Rozendaal & Dekker (1989), Stresemann (1940), Wardill (1995), Watling (1983), White & Bruce (1986).

30. Sangihe Scops-owl

Otus collari

French: Petit-duc de Sangihe **German:** Sangiheule **Spanish:** Autillo de la Sangihe

Taxonomy. *Otus collari* Lambert and Rasmussen, 1998, Sangihe Island, Indonesia.

Probably forms superspecies with *O. elegans* and *O. manadensis*. Original specimens, collected in 1866 and 1867, thought to be same species as *O. manadensis*. Subsequent authors placed it very tentatively with *O. magicus*, though without critical examination of specimens, and more recently again with *O. manadensis*, still without real knowledge of vocalizations or morphology. Later, in 1996, photographs and taped vocalizations revealed some differences from both *O. manadensis* and *O. magicus*; despite strong similarities with some individuals of *O. manadensis*, sufficient and constant morphological and vocal differences support treatment as separate species. Monotypic.

Distribution. Sangihe I, N of Sulawesi.



Descriptive notes. c. 19.5 cm; male 76 g. Rather small, generally brownish scops-owl with moderate-length ear-tufts, relatively long tail and long, narrow wings; relatively small, weak toes and claws. Facial disc brownish-white with dark lores and short whitish eyebrows; upperparts drab brown with dark shaft streaks and conspicuous buff spots, scapulars with black-tipped whitish and buff spots; flight-feathers and tail barred dark brown and buff; underparts somewhat paler, with prominent black shaft streaks and fine vermiculations; tarsus almost fully feathered; iris yellow; bill horn-brown; toes pale grey or pale brown. Differs from all *O. manadensis* in considerably longer, narrower wings, slightly longer tail, and combination of drabber appearance, paler facial disc with shorter, less obvious eyebrows, more contrasting narrower dark crown streaks, more coarsely mottled upperparts, plainer wing-coverts, reduced barring below with pale areas smaller, weaker feet; smaller than *O. magicus*, differing from small races *albiventer* and *tempestatis* of latter in shorter eyebrows, lack of solid dark ear-covert patch, broader dark bands on tail. Juvenile undescribed. Voice. High-pitched, downslurred, fluty whistle, "kleeeer", c. 0.7-0.8 seconds long, repeated at intervals of 8-15 seconds; also faster version, c. 3 notes per second.

Habitat. Forest, mixed plantations, secondary growth; also agricultural areas with trees and bushes. From sea-level to at least 315 m.

Food and Feeding. No information.

Breeding. No information.

Movements. Presumably resident.

Status and Conservation. Not globally threatened. CITES II. Appears fairly widespread within single-island range, with records from various localities throughout, but no data on numbers. Observations show that species readily tolerates man-altered habitats, occurring especially in mixed plantations, a habitat type which has for many decades been a major feature of the island's landscape. No obvious threats; in view of highly restricted range and lack of real knowledge of its ecology, however, species should perhaps be placed in category of Vulnerable.

Bibliography. Anon. (1999), Lambert & Rasmussen (1998), Riley (1997a, 1997b), Sangster (1999).

31. Biak Scops-owl

Otus beccarii

French: Petit-duc de Beccari **German:** Beccarieule **Spanish:** Autillo de Biak
Other common names: Beccari/Papuan Scops-owl

Taxonomy. *Scops beccarii* Salvadori, 1875, Misori.

Sometimes treated as conspecific with either *O. manadensis* or *O. magicus*; song similar to latter's, but significant differences from both in plumage. Monotypic.

Distribution. Biak I, off NW New Guinea (Irian Jaya).

Descriptive notes. c. 20 cm. Occurs in dark brown and dark rufous-brown forms; almost certainly morphs, but sometimes interpreted as sexual difference. Facial disc pale whitish-brown, edged darker,



with short white eyebrows; forecrown with few indistinct dark streaks; entire upperparts, including crown and ear-tufts, densely barred, bars on nape more distinct; scapulars with largely white outer webs, some black at tips; flight-feathers and tail barred; underparts vermiculated black and white on brownish ground, or deep rufous with less obvious vermiculations, undertail-coverts white with some broken rufous and black bars; tarsus feathered to toes; iris yellow; bill grey; feet yellowish. Distinguished from all other *Otus* by lack of streaking above and below. Juvenile not described. **VOICE.** Hoarse, corvid-like

croak, repeated in series; at close range, described as "a quite disagreeable rasp".

Habitat. Forest and forest edge; also heavily wooded areas, locally near villages.

Food and Feeding. Insects; possibly some small vertebrates.

Breeding. No information.

Movements. Presumably resident.

Status and Conservation. Not globally threatened. CITES II. Very poorly known. A survey conducted in 1973 on Biak found only 1 pair of this species, in the only undisturbed forest left on the island. Conservation status probably overlooked owing to its having frequently been treated as race of more widespread and commoner *O. magicus*. In view of very small range and apparent diminution of habitat, this species should probably be considered at best Vulnerable.

Bibliography. Beehler *et al.* (1986), Clark & Mikkola (1989), Iredale (1956), King (1978/79), Marshall (1978), Mayr & Meyer de Schauensee (1939a), Rand & Gilliard (1967).

32. Seychelles Scops-owl

Otus insularis

French: Petit-duc scieur

German: Seychelleneule

Spanish: Autillo de Seychelles

Other common names: Bare-legged Scops-owl

Taxonomy. *Gymnoscops insularis* Tristram, 1880, Mahé Island, Seychelles.

Originally placed in monotypic genus *Gymnoscops* on basis of its unfeathered tarsi and feet, and vestigial ear-tufts. Formerly considered race of *O. rutilus*, but vocalizations totally dissimilar. Sometimes treated as race of *O. magicus*, this supported by voice comparisons, but long isolation from all forms of latter, as well as morphological differences, suggest better regarded as separate species. Monotypic.

Distribution. Mahé I, in Seychelles. Unconfirmed reports also from Praslin and Félicité.



Descriptive notes. c. 20 cm. Resembles yellowish-brown or rufous morph of *O. magicus*, but smaller, and with minute ear-tufts (even in alert posture); differs further in unfeathered tarsus, often more buffish coloration, more prominent rim to facial disc, more distinct large black spots on crown and nape. Juvenile similar to adult. **VOICE.** Deep saw-like croak, "waugh", repeated every 3-4 seconds, also series of knocking "tok tok tok" sounds, the two sometimes interspersed; sequence may last up to 20 minutes.

Habitat. Virtually all records from secondary forest on upper slopes and in valleys, at 250-600 m above sea-level, usually close to water

source; thought originally to have inhabited lowland forest and woodland as well, before these latter destroyed.

Food and Feeding. Insects, tree frogs and lizards probably most important prey; stomach contents included grasshoppers, beetles, lizards, and some vegetable matter. Strictly nocturnal.

Breeding. Data few and sparse, with much speculation. High-pitched whistle apparently given during copulation, heard frequently in Oct and Apr, and fledged young seen in Nov and Jun, suggesting twice yearly breeding cycle. No nest found, but favours boulder fields in forest and spends much time on ground; subterranean nesting suspected, perhaps cleft in rocks. Clutch size unknown; 2 adults observed with presumed fledgling, suggesting that clutch may be reduced to single egg.

Movements. Resident.

Status and Conservation. CRITICALLY ENDANGERED. CITES II. Restricted-range species; present in Granitic Seychelles EBA. Following its discovery in 1880, and despite a specimen collected in 1940, no others sighted for over half a century; declared extinct in 1958. Its rediscovery on Mahé in 1959 led to speculation that 20 birds may remain on the island; studies in mid 1970's confirmed presence of 12 pairs, extrapolation from which suggested total population of perhaps over 80 pairs, possibly twice that; in mid 1990's, preliminary estimate of 90-180 territories. Local inhabitants of Mahé commonly report calls, perhaps suggesting that species more numerous than thought. Earlier reports of possible presence on Praslin and nearby Félicité I unconfirmed. Major threats are habitat destruction for housing development and timber exploitation, with new logging techniques making more areas accessible, e.g. upper Grand Bios Valley (where species known to exist), and probably introduced predators such as cats and rats. Some conservation measures already taken; Mome Seychellois National Park includes much of highland forest in its range, but extension of its boundaries desirable. Monitoring by means of controlled tape-luring can be used to determine distribution and status; more complete understanding of species' ecology and biology, especially breeding habits, required before degree of threat can be assessed and conservation measures successfully implemented. Speculation that introduced Common Barn-owl (*Tyto alba*) may compete for food considered improbable.

Bibliography. Bullock (1990), Clark & Mikkola (1989), Collar & Andrew (1988), Collar & Stuart (1985), Collar *et al.* (1994), Diamond & Feare (1980), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Evans (1977), Gaymer *et al.* (1969), Gerlach (1997), Greenway (1967), Keith (1980), Kemp & Kemp (1998), King (1978/79), Loustau-Lalanne (1962), Marshall (1978), Penny (1968, 1974), Rocamora & Skerrett (1999), Shuker (1993), Sinclair & Langrand (1998), Stattersfield *et al.* (1998), Watson (1979, 1980), Wilson (1981).

33. Simeulue Scops-owl

Otus umbra

French: Petit-duc de Simalur

German: Simalureule

Spanish: Autillo de la Simeulue

Other common names: Mentauf/Simalur/Simulu Scops-owl

Taxonomy. *Pisorhina umbra* Richmond, 1903, Simalur Island.

Probably forms superspecies with *O. enganensis* and *O. alius*. Previously considered race of either *O. scops* or *O. sunia*. Sometimes treated as conspecific with *O. enganensis*, but vocalizations apparently very different. Monotypic.

Distribution. Simeulue I, off NW Sumatra.



Descriptive notes. 16-18 cm; c. 90-100 g. Overall reddish-brown with shortish ear-tufts, rounded wing; facial disc paler, plain rufous; crown with few thin shaft streaks; upperparts finely vermiculated with black, scapulars with black-edged whitish outer webs; flight-feathers and tail barred; underparts slightly paler than upperparts, with whitish vermiculations and rufous barring with occasional black shaft streaks within; tarsus feathered almost to toes; iris yellow to greenish-yellow; bill and feet grey. Differs from *O. sunia* in paler bill, fewer shaft streaks, darker belly, smaller ear-tufts; from *O. enganensis* in smaller size, with

smaller feet and claws, less heavily feathered tarsi. Juvenile undescribed. **VOICE.** Male territorial call two steady notes followed by higher and rising note, "pook-pook-pupook", repeated at varying intervals; in duet, female higher-pitched, can occasionally sound like long whine.

Habitat. Forest edge and remnant forest on steep slopes, especially coastal forest; noted also in clove plantations.

Food and Feeding. Probably mostly insects.

Breeding. Recorded singing on clear nights in Mar; no other information.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Reports of status differ; usually said to be rare or "possibly rare", but one source clearly states that it is not rare. Poorly studied, and no indication of population numbers. Restricted to single island, main threat presumably habitat destruction.

Bibliography. Andrew (1992), Holmes, D.A. (1994a), Inskipp *et al.* (1996), MacKinnon & Philipps (1993), van Marle & Voous (1988), Marshall (1978), Richmond (1903), Stattersfield *et al.* (1998).

34. Enggano Scops-owl

Otus enganensis

French: Petit-duc d'Enggano

German: Engganoeule

Spanish: Autillo de la Enggano

Taxonomy. *Otus umbra enganensis* Riley, 1927, Enggano Island.

Probably forms superspecies with *O. umbra* and *O. alius*. Sometimes considered conspecific with *O. magicus*. Formerly treated as race of *O. umbra*, *O. scops* or *O. sunia*; seems closest to *O. umbra*, but separated specifically on basis primarily of vocal characteristics. Monotypic.

Distribution. Enggano I, off SW Sumatra.



Descriptive notes. 16-20cm. Very similar to *O. umbra*; differs in slightly more distinct dark markings, especially on crown and wings, duller and darker upperparts, more marked whitish eyebrows, hint of pale nuchal collar, slightly larger size. Juvenile undescribed. **VOICE.** Apparently rather similar to that of *O. magicus* and said to differ from *O. umbra*, but descriptions lacking.

Habitat. Very poorly recorded; presumably similar to that of *O. umbra*, occupying forest edge and wooded areas.

Food and Feeding. Probably mainly insects; no information.

Breeding. No information.

Movements. Presumably resident.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Enggano EBA. Reports on status vary widely, ranging from very rare to quite common; several different individuals were seen during a short visit to the island in 1983; very poorly studied. So far, habitats on Enggano relatively undisturbed, but recent tentative proposals for agricultural investments indicate possible risk of drastic changes in habitat in future.

Bibliography. Andrew (1992), Holmes, D.A. (1994a), Inskipp *et al.* (1996), Junge (1938), MacKinnon & Philipps (1993), van Marle & Voous (1988), Stattersfield *et al.* (1998), Sujatnika *et al.* (1995).

35. Nicobar Scops-owl

Otus alius

French: Petit-duc de Nicobar

German: Nicobareule

Spanish: Autillo de Nicobar

Taxonomy. *Otus alius* Rasmussen, 1998, Campbell Bay, Great Nicobar.

Probably forms superspecies with *O. umbra* and *O. enganensis*. Original specimen collected in 1966 initially listed as race (*nicobaricus* = *modestus*) of *O. sunia*, though long wings unlike all forms of that species; second specimen collected in 1977, and the two suspected of belonging to an undescribed taxon, tentatively placed with an "expanded" *O. magicus*. Subsequently treated as race *nicobaricus* (= *modestus*) of *O. sunia*, or as a form of *O. magicus* without subspecific allocation, but in one case listed as "*Otus* sp.". Recent examination of both specimens, along with comparisons with all other *Otus* taxa of non-mainland SE Asia (N to Philippines), led to conclusion that they were sufficiently distinct in plumage and morphology to warrant recognition as separate species. Monotypic.

Distribution. Great Nicobar I, southernmost of Nicobar Is.

Descriptive notes. c. 19-20 cm. Warm brown scops-owl, finely but distinctly barred all over, unstreaked above and with greatly reduced streaking below; mid-length ear-tufts finely barred; facial disc paler, lightly barred at lower edge, with indistinct outer border; rounded white scapular spots tipped black; iris conjecturally yellow, but no definite information; bill mostly brownish, medium-sized; lowermost part of tarsus, and much of its rear edge, unfeathered; toes and claws relatively large. Differs from all other Asian taxa of *Otus* in combination of finely barred plumage, with streaking totally lacking above and almost so below, underside being heavily barred whitish.



cinnamon and dusky brown, and relatively large claws; distinguished from geographically closest *O. umbra* in larger size, less rufous-toned plumage, paler facial disc, barred ear-tufts, larger black tips to scapulars, and proportionately much bigger feet and claws. **VOICE.** Male unknown. Female said to have given protracted melancholic moan on rising scale, "ooo-m" or "ooün", 2-2.5 seconds long, repeated after 3-5 seconds, uttered continuously for over 30 minutes.

Habitat. Both specimens collected in coastal forest, near sea-level.

Food and Feeding. One noted to have eaten a spider and a beetle; stomach contents of other bird included a 10-cm gecko.

Breeding. Male specimen had greatly enlarged testes on 3rd Mar; female specimen approaching breeding condition on 2nd Apr. No other information.

Movements. No information. Presumably resident.

Status and Conservation. Not globally threatened. CITES II. Very poorly studied species, not yet listed in any threat category simply because only very recently described; known from only 2 specimens, both from same site (Campbell Bay) on comparatively small island; no other records. Species may possibly occur on nearby islands, e.g. Little Nicobar a few km to N, but these areas barely studied by ornithologists; not found on the few pre-1966 expeditions to Nicobars. Nothing known of its ecology or biology. Probably a rare species, which should be considered at very best Vulnerable and more likely Endangered.

Bibliography. Abdulali (1967, 1978), Ali & Ripley (1981), Rasmussen (1998b), Ripley (1982), Sangster (1998), Sankaran (1998).

36. Pemba Scops-owl

Otus pemaensis

French: Petit-duc de Pemba

German: Pembaeule

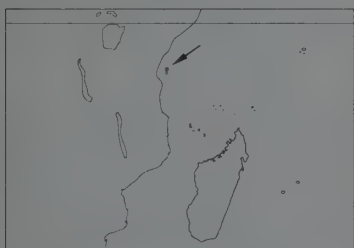
Spanish: Autillo de Pemba

Other common names: Russet Scops-owl

Taxonomy. *Otus pemaensis* Pakenham, 1937, Wete, Pemba.

Relationships unclear. Often treated as race of *O. rutilus*. Monotypic.

Distribution. Pemba I, off N Tanzania.



Descriptive notes. c. 16 cm. Small scops-owl with small ear-tufts. Occurs in rufous and brown morphs, with intermediates varying considerably in colour. All have pale scapular spots and light eyebrows of varying prominence, and barred primaries but unbarred tail; dark rufous individuals usually unmarked; light rufous birds with some streaks on crown, some vague broad barring below, and few fine streaks on flanks; brown morph fairly uniform rufous-brown, unbarred above, dusky streaks on crown, creamy facial disc, pale below with fine vermiculations and thinly streaked breast and flanks, lower abdomen with more rufous and

white barring; tarsal feathering heavy and barred, reaching toes; iris yellow; bill dull greenish to yellow-grey with black tip; toes grey. Differs from *O. rutilus* in smaller size, much more uniform plumage. Juvenile colour morph immediately evident; pale young vaguely barred cinnamon, much more prominently barred on crown and tail. **VOICE.** Monosyllabic "hu" given at irregular intervals, or in fast runs of 4-6 in 10 seconds; in duet, male lower-pitched than female; similar to *O. rutilus*, but different timbre, less regular intervals. Calls start at sunset and continue until darkness.

Habitat. Well-wooded areas with densely foliated trees, often in clove and mango plantations. Roosts in dense undergrowth, at times quite low down c. 2 m from ground, and rarely stirring by day; reported to sit so tightly as to allow itself to be picked up.

Food and Feeding. Mainly insects. Hunts from perch, dropping on to prey; also gleans from foliage or hawks insects in flight. Nocturnal.

Breeding. Male with active gonads collected Aug; may breed Aug-Oct. Nest probably in tree cavity; reports of nests in heaps of dead branches and leaves on ground considered highly improbable. Virtually nothing recorded.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Pemba EBA. Currently considered Near-threatened. Appears to be fairly common and widespread, especially in clove plantations, in its restricted range, but no indication of population levels. Biology fairly unknown, warrants further study. Natives of Pemba said to identify this species with witchcraft and once thought it to be viviparous; unknown how this reflects or influences its numerical status, but human persecution a distinct possibility.

Bibliography. Bennun & Njoroge (1996), Britton (1980), Brown (1977), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Fry *et al.* (1988), Kemp & Kemp (1998), Mackworth-Præd & Grant (1957), Pakenham (1939, 1979), Short *et al.* (1990), Snow (1978), Stattersfield *et al.* (1998), Zimmerman, D.A. *et al.* (1996).

37. Comoro Scops-owl

Otus pauliani

French: Petit-duc du Karthala

German: Komoreneule

Spanish: Autillo de las Comores

Other common names: Grand Comoro Scops-owl

Taxonomy. *Otus rutilus pauliani* Benson, 1960, La Convalence, 1700 m, Grand Comoro.

Probably forms superspecies with *O. capnodes*, *O. moheliensis* and *O. rutilus*. Often considered race of *O. rutilus*, but clear differences in vocalizations, morphology and habitat preferences indicate separate species. Monotypic.

Distribution. Mt Karthala on Grand Comoro (Njazidja), in Comoro Is.

Descriptive notes. 15-20 cm; male c. 70 g. Small, relatively uniform scops-owl, with very small ear-tufts rarely visible in the field. Occurs in light and dark morphs. Grey or brown facial disc speckled with white, with some darker rings, and faint pale eyebrows; upperparts dark grey-



brown or brown with indistinct paler barring, scapulars inconspicuously spotted buff; wings and tail barred; underparts light to dark rufous-brown, densely vermiculated darker, with sparse and variably distinct black shaft streaks; lower tarsus unfeathered; iris yellow or dark brown; bill grey-brown; legs and feet brownish. Distinguished from *O. rutilus* by smaller size, almost no ear-tufts, finely barred, unstreaked plumage, less extensively feathered tarsus, and very small bill. Juvenile unknown. **VOICE.** High whistled "toot" or "choo" at regular intervals of 1-2 seconds, quickly turning into faster series of shorter down-

slurred "cho" notes repeated at half-second intervals for 10 minutes; female also drawn-out "choeiet" in duet.

Habitat. Forest and forest edge on upland slopes, extending into adjoining tree-heath scrub; recorded at 1000-1800 m, but recently reported at lower levels.

Food and Feeding. Largely unknown, probably insects; 1 stomach contained beetle remains. Species' weak talons suggest that it normally takes invertebrates.

Breeding. Probably lays Sept-Dec; very vocal throughout year. Highly territorial, territory size c. 5 ha. Nest in cavity.

Movements. Probably sedentary.

Status and Conservation. CRITICALLY ENDANGERED. CITES II. Restricted-range species; present in Comoro Islands EBA. A minimum of c. 1000 pairs may exist within the estimated 100 km² of suitable habitat remaining on Mt Karthala. Population seems stable and perhaps not under such great threat as feared, but deforestation is slowly creeping up the mountainside. Strongholds in areas where terrain too rocky to be cleared for agriculture. Situation may worsen in the future, with local deforestation causing increased fragmentation of habitat, and further destruction from practice of burning to obtain grazing land for cattle; clearance and cattle grazing make conditions more favourable for the introduced Common Myna (*Acridotheres tristis*), which competes with present species for nest cavities. Proposal for a nature reserve on Mt Karthala should be implemented immediately.

Bibliography. Benson (1960), Clark & Mikkola (1989), Collar & Andrew (1988), Collar & Stuart (1985), Collar *et al.* (1994), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Herremans (1988), Herremans *et al.* (1991), Hornbuckle (1997), Kemp & Kemp (1998), Louette (1984, 1988a, 1992), Louette & Stevens (1992), Louette, Herremans *et al.* (1990), Louette, Stevens *et al.* (1988), Shuker (1993), Sinclair & Langrand (1998), Snow (1978), Stattersfield *et al.* (1998).

38. Anjouan Scops-owl

Otus capnodes

French: Petit-duc d'Anjouan

German: Anjouaneule

Spanish: Autillo de Anjouan

Other common names: Smoky Scops-owl

Taxonomy. *Scops capnodes* Gurney, 1889, Anjouan.

Probably forms superspecies with *O. pauliani*, *O. moheliensis* and *O. rutilus*. Sometimes treated as race of *O. rutilus*, but analysis of vocalizations and plumage characters indicates specific status appropriate. Monotypic.

Distribution. Anjouan (Ndzuani), in Comoro Is.



Descriptive notes. c. 22 cm; male 119 g. Smallish scops-owl with very small ear-tufts. Occurs in dark grey-brown and rufous-brown morphs. Rufous morph with head dusky brown with white spotting, facial disc creamy with whitish eyebrows, upperparts brown to rufous-brown with fine buffish bars and spots, flight-feathers barred, underparts paler with dark shaft streaks and finely vermiculated with sepia, buff and cream. Dark morph dark chocolate-brown to grey-brown, no white in plumage, finely grizzled as opposed to barred or streaked. Tarsus with distal third bare; iris greenish-yellow; bill horn-grey to grey-green;

feet yellowish-grey. Distinguished from *O. rutilus* by darker appearance, no pale scapular stripe, much less obvious ear-tufts, longer wings. Juvenile undescribed. **VOICE.** Prolonged whistle, "peeoeoe" or "peeoo", recalling Grey Plover (*Pluvialis squatarola*), repeated 3-5 times at intervals of 0.5-1.5 seconds; also long harsh screech; sometimes calls during day.

Habitat. Restricted to remnant primary forest on mountain slopes above 550 m, mostly above 800 m; no records from exotic plantations in foothills. Perches usually in dense vegetation, 3-15 m above ground; roosts in holes in large trees.

Food and Feeding. No definite information; probably insects.

Breeding. No confirmed data. Nest probably in cavity in thick tree trunk, e.g. where branch broken off; several records of bird seen perched at entrance of such sites.

Movements. No information; presumably sedentary, with only local movements.

Status and Conservation. CRITICALLY ENDANGERED. CITES II. Restricted-range species; present in Comoro Islands EBA. Speculation that over-collecting in late 1800's might have caused its extinction was unfounded, as the number of specimens collected was relatively small, and the species survives well so long as its habitat is available; its apparent "disappearance" was due largely to its being overlooked as a result of its vocalizations being very unlike those associated with owls, and it has always been well known to local people. Very local, but reasonably common on steep forested slopes; on basis of confirmed sightings and known habitat preferences, population estimated at possibly 100-200 pairs. Clearing of primary forest and replacement by exotic plantations presumed biggest threat; remaining suitable habitat scarce, totalling only c. 10-20 km². Species also hunted for food, rendering surviving population even more threatened. Speculated also that introduced rats may affect breeding success. No known conservation measures taken, and no protected areas on Anjouan. Urgent action recommended. Possibility of captive breeding recently suggested, but capturing of wild birds, which are prized as human food, in such a vulnerable habitat could cause further problems.

Bibliography. Anon. (1992b), Benson (1960), Clark & Mikkola (1989), Collar *et al.* (1994), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Greenway (1967), Herremans (1988), Hornbuckle (1997), Kemp & Kemp (1998), King (1978/79), Knox & Walters (1994), König, P. (1995), Lewis (1996), Louette (1988a),

Louette *et al.* (1988), Safford (1993), Sayers (1998b), Shuker (1993), Sinclair & Langrand (1998), Snow (1978), Stattersfield *et al.* (1998).

39. Moheli Scops-owl

Otus moheliensis

French: Petit-duc de Mohéli **German:** Mohelieule **Spanish:** Autillo de Moheli

Taxonomy. *Otus moheliensis* Lafontaine and Moulart, 1998, Mohéli.

Very recently discovered species. Probably forms superspecies with *O. pauliani*, *O. capnodes* and *O. rutilus*. Monotypic.

Distribution. Mohéli (Mwali), in Comoro Is.



Descriptive notes. c. 22 cm, male 95 g, female 116 g. Fairly uniform-looking scops-owl with greatly reduced ear-tufts. Occurs in brown and rufous morphs. Brown morph rufescent-brown, spotted and barred blackish on crown and upperparts, especially on nape, with some blackish shaft streaks; scapulars with paler cinnamon outer webs; facial disc and underparts more rusty-cinnamon, breast with blackish shaft streaks, flanks and belly with fine darker bars. Rufous morph similar, but more rufous-cinnamon all over. Lower third of tarsus unfeathered; iris yellow; bill horn; lower tarsus and feet grey. Juvenile undescribed. Voice.

Poorly known; male said to give series of 1-5 hissing whistles; a screech also described.

Habitat. Dense humid forest on hillsides; also at lower densities in degraded forest; recorded at 450-790 m.

Food and Feeding. Probably insects.

Breeding. No information.

Movements. Presumably resident.

Status and Conservation. Not globally threatened. CITES II. Appears at present to be common in forested uplands, with c. 1 bird/5 ha in undisturbed forest; in degraded parts, 1 bird/10 ha. Current population estimated at c. 400 individuals. Main problem is habitat loss; forest being gradually destroyed for agriculture, with no sign of clearance ceasing; in 1995 dense humid forest restricted to 1070 ha (or 5% of the island's surface area), while between 1955 and 1968 it was estimated at 5000-6000 ha (30%). Species not yet listed in any threat category simply because only recently discovered; should probably be placed in Endangered category.

Bibliography. Anon. (1998c, 1998g), Lafontaine & Moulart (1998, 1999), Moulart (1998).

40. Madagascar Scops-owl

Otus rutilus

French: Petit-duc malgache **German:** Madagaskar-Zwergohreule **Spanish:** Autillo Malgache
Other common names: Malagasy/Ruddy Scops-owl

Taxonomy. *Scops rutilus* Pucheran, 1849, Madagascar.

Probably forms superspecies with *O. pauliani*, *O. capnodes* and *O. moheliensis*. Has been considered to include first two, as well as *O. pambensis* and *O. insularis*, as races; vocal comparisons and morphology (size, plumage markings, extent of tarsal feathering) indicate that all are specifically distinct. Race *mayottensis* possibly sufficiently distinct to merit full species status; more study needed. Population in drier W Madagascar apparently an unrecognized taxon; further research in progress. Two subspecies currently recognized.

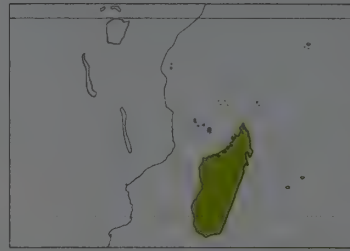
Subspecies and Distribution.

O. r. mayottensis Benson, 1960 - Mayotte I (Comoro Is).

O. r. rutilus (Pucheran, 1849) - Madagascar.

Descriptive notes. 22-24 cm; wingspan 53 cm; male 85-107 g, female c. 112 g. Occurs in grey, brown and rufous morphs, with many intermediates; extremely variable. Facial disc pale, darker around eyes, with off-white eyebrows; crown and upperparts grey-brown to brown, often tinged rufous, with buffish spots and black shaft streaks, scapulars with black-edged white spots; flight-feathers and tail barred; paler below, with bold blackish streaks and faint vermiculations, breast centre sometimes plain whitish, also abdomen. Rufous morph strongly tinged rufous all over, sometimes nearly lacking black markings. Tarsus feathered to toes; iris yellow; bill largely blackish; toes grey-brown. Juvenile similar to adult. Race *mayottensis* slightly larger, darker, with bigger ear-tufts, more prominently white chin and lores, less white on abdomen; birds in dry parts of W Madagascar average greyer and less boldly marked. Voice. Fast series of 5-15 short, even-pitched "hoo" or "broo" notes, increasing slightly in volume, last 2 notes softer, whole phrase lasting 1.5-5 seconds, repeated after some seconds; in dry areas of W, shorter, slower series of 3-7 more tremulous, lower-pitched notes, phrase 2-3 seconds; *mayottensis* similar to E Madagascar birds, but notes a bit longer and deeper, sequence slower.

Habitat. Variety of habitats, ranging from primary and secondary forest to thickets, humid bush country and urban parks, and not uncommon in trees around villages; avoids exotic plantations; in



W & SW Madagascar, also drier forest. Spends daytime concealed in thick foliage, sometimes low down. Sea-level to 2000 m. Recorded in lowland secondary forest on Mayotte.

Food and Feeding. Mostly insects, especially beetles and moths; possibly some small vertebrates. Strictly nocturnal.

Breeding. Lays Nov-Dec. Nest in tree cavity, occasionally in abandoned stick nest of other bird. 4-5 eggs; incubation and fledging periods unknown.

Status and Conservation. Not globally threatened. CITES II. Generally common and widespread in suitable habitat throughout range.

Reported as common to abundant e.g. in forested areas between Betsileo and Tanala, forest of Ankafana, and near Zahamena. Rare in woodlands of the high plateau near Ambositany, Antananarivo. Occurs in several protected areas, e.g. Ranomafana National Park, Perinet Special Reserve and Berenty Private Reserve.

Bibliography. Appert (1996), Benson *et al.* (1976-1977), Dee (1986), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Goodman & Parrillo (1994), Goodman *et al.* (1997), Herremans (1988), Hornbuckle (1997), Kemp & Kemp (1998), Langrand (1995), Lewis (1998), Louette (1988c), Marshall (1978), Milon *et al.* (1973), Morris & Hawkins (1998), Ramanitra (1995), Rand (1936), Safford & Duckworth (1990), Sinclair & Langrand (1998), Snow (1978), Young (1995).

41. Sao Tome Scops-owl

Otus hartlaubi

French: Petit-duc de Sao Tomé **German:** Hartlaubeule **Spanish:** Autillo de Santo Tomé

Taxonomy. *Noctua Hartlaubi* Giebel, 1872, São Tomé Island.

Affinities uncertain. May be more closely related to *O. rutilus* than to any mainland African species, though song fairly similar to that of *O. senegalensis*; formerly suggested as race of *O. scops*, but differs significantly in morphology and voice. Monotypic.

Distribution. São Tomé I; report of possible presence on Príncipe.



Descriptive notes. 16-19 cm; c. 80 g. Small scops-owl with tiny ear-tufts. Facial disc light rufous-brown, with white chin and eyebrows; crown and upperparts warm rufous-brown with rufous vermiculations and blackish shaft streaks, scapulars with black-tipped white spots; flight-feathers mottled with buff and white, tail with narrow buff bars; underparts finely vermiculated with brown, rufous and white, and bold black streaking; tarsus unfeathered; iris and bill yellow. A grey-brown morph has been described, but apparently very rare. Juvenile paler, finely barred light brown above and below. Voice. High whistling trill,

"hu-hu-hu-...", rising slightly, higher-pitched and more mellow than that of *O. scops* or *O. senegalensis*, given at intervals of 15-20 seconds; also low, harsh "kwo". Heard by day, as well as at dusk and night.

Habitat. Densely foliated primary and secondary forest, and plantations, to 1300 m above sea-level; densities highest in secondary forest and clove and mango plantations at c. 400 m.

Food and Feeding. Stomach contents indicate insects, such as grasshoppers, beetles and moths; some small lizards also taken. Appears to be partly diurnal. Forages in lower parts of forest; hunts from perch 1.5-10 m above ground, dropping on to prey; also gleans from foliage or hawks prey in flight; occasionally descends to ground.

Breeding. Male with active gonads in Aug, fledglings observed in Oct; may breed before start of short rains during Aug-Oct. No other information.

Movements. Presumably resident.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in São Tomé EBA. Currently considered Near-threatened. Poorly known, and for some time thought to be rare, but on protracted visits to forest areas found to be common, e.g. in dense secondary vegetation bordering Io Grande R; distribution appears highly fragmented, but factors responsible for its absence from some parts unknown; seems able to accept some modification of habitat on edge of its range, and will recolonize areas abandoned after cultivation, but shuns shaded cocoa and coffee plantations. No figures available on population; competition from Common Barn-owls (*Tyto alba*) and predation by cats possibly reducing species' numbers; pesticides heavily used on São Tomé during 1963-1973, probably had adverse effect. Studies of species' biology and population level much needed.

Bibliography. Amadon (1953), Atkinson, Dutton *et al.* (1994), Christy (1998), Clark & Mikkola (1989), Collar & Andrew (1988), Collar & Stuart (1985), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Fry *et al.* (1988), Jones & Tye (1988), Jones *et al.* (1992), Kemp & Kemp (1998), Mackworth-Praed & Grant (1970), Marshall (1978), de Naurois (1975, 1994b), Sargeant (1994c), Snow (1950, 1978), Stattersfield *et al.* (1998).



PLATE 8

inches 4
cm 10

- grey-brown morph
- ssp kennicottii
- rufous-buff morph
- 43
- ssp cooperi
- ssp lambi
- 44
- ssp vinaceus
- 42
- ssp xantusi
- 45
- ssp asio
- grey-brown morph
- rufous morph
- ssp maxwelliae
- 46
- ssp trichopsis
- rufous morph
- grey-brown morph
- 47
- ssp mesamericanus
- rufous morph
- 48
- ssp roboratus
- 49
- ssp pacificus
- 50
- 51
- brown morph
- rufous morph

42. Western Screech-owl

Otus kennicottii

French: Petit-duc des montagnes **German:** Westkreischeule **Spanish:** Autillo Californiano
Other common names: Kennicott's Screech-owl; Vinaceous Screech-owl (*vinaceus*)

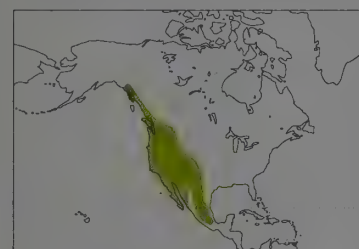
Taxonomy. *Scops Kennicottii* Elliot, 1867, Sitka, Alaska.

Sometimes considered to form superspecies with *O. seductus*, *O. cooperi* and *O. asio*. Formerly treated as conspecific with *O. asio*, and may interbreed where ranges meet or overlap (separated by 60 km in Oklahoma "panhandle", slightly sympatric in Colorado Springs, broadly overlapping in Texas, areas of contact in Mexico undetermined); vocal and DNA analyses, however, show that better treated as separate species. Often considered to include *O. seductus* and *O. cooperi* as races. Race *vinaceus* has been proposed as a megasubspecies. Geographical limits of listed races uncertain, with intergrades at boundaries. Many additional races described, but some probably reflect individual variation only: *saturatus* included in nominate *kennicottii*; *macfarlanei* and *brewsteri* in *bendirei*; *mychophilus*, *inyoensis* and *cineraceus* in *aikeni*; *quercinus*, *clazus* and *gilmani* in *cardonensis*; *sortilegus* in *suttoni*; and *sinaloensis* in *vinaceus*. Eight subspecies recognized.

Subspecies and Distribution.

- O. k. kennicottii* (Elliot, 1867) - coast from S Alaska and NW Canada to NW California.
- O. k. bendirei* (Brewster, 1882) - E Washington and Montana S to SE California.
- O. k. aikeni* (Brewster, 1891) - from SW USA (California E to W Oklahoma) S to N Mexico (NC Sonora).
- O. k. cardonensis* Huey, 1926 - S California and N Baja California.
- O. k. xantusi* (Brewster, 1902) - S Baja California.
- O. k. yumanensis* A. H. Miller & L. Miller, 1951 - SE California and SW Arizona to N Mexico (NW Sonora).
- O. k. suttoni* R. T. Moore, 1944 - SW Texas S to Mexican Plateau.
- O. k. vinaceus* (Brewster, 1888) - Mexico (S Sonora and W Chihuahua to N Sinaloa).

Descriptive notes. 21-24 cm; male 131-210 g, female 157-250 g. Occurs in grey-brown and rufous-buff morphs; latter generally subdued cinnamon-buff, found in N of range, rare elsewhere. Facial disc predominantly whitish, with thin dark margin; neck region light tawny to white; upperparts with dark shaft streaks, more prominent on head than on back, and faint thin vermiculations; often purplish tint above, especially on wings; scapulars with black-edged whitish outer webs forming pale shoulder line; flight-feathers strongly barred; underparts lighter than upperparts, prominently streaked dark, with streaks crossed by much thinner bars



or spots, markings heavier on breast than on flanks; tarsus fully feathered; iris yellow; bill blackish; toes grey-brown. Distinguished from *O. asio* and *O. trichopsis* by darker bill, less coarse streaking below, and much bigger than *O. trichopsis*. Juvenile deep grey-brown above, indistinctly and rather broadly barred with dusky, dull white below, broadly barred greyish-dusky. Races differ in plumage colour, streaking and size, but highly variable, generally paler in more arid regions: *bendirei* longer-winged than nominate; *cardonensis* darkish, more densely marked; *suttoni* darkest; *vinaceus* somewhat smaller, paler with vinaceous wash, vermiculations below in form of reddish dots; *yumanensis* pale pinky-grey; *aikeni* palest grey; *xantusi* almost as pale, smallest. Voice. Primary song a double trill, first short and second long, dropping near end; secondary song accelerating series of c. 5-15 soft hoots, final notes run together, in bouncing-ball rhythm; female higher-pitched; duets last 2-4-5 seconds.

Habitat. Open woodland, semi-open country with scattered trees and bushes, riparian forest, cactus desert, also parks and larger gardens in suburban areas; some preference for pine-oak forest. In general, prefers open tree or cactus growth with abundance of insects and small mammals, available cavities, and environmental factors with which its plumage coloration blends well. In Oregon, found to inhabit riparian zones, abandoned homesteads, and some cliffs; in Idaho, riparian areas with abundant deciduous cover 4-8 m tall; often uses river-bottom and bunch-grass habitat, or may opt for mixture of coniferous and deciduous habitats; locally, occurs in stands of giant cardon and saguaro (*Carnegiea*) cacti in upland desert, in Joshua trees (*Yucca*), in stands of sycamore (*Acer*) and cottonwood (*Populus*), tamarisk (*Tamarix*) and willow (*Salix*) along rivers, in groves of mesquite (*Prosopis*), in open pinyon-juniper woodland or pine forest, and atypically in low, dense Douglas fir (*Pseudotsuga*) forest. Prefers to roost among denser trees, sometimes next to trunk; after leaf fall, will also roost in nestboxes or cavities.

Food and Feeding. Insects, small mammals (rodents, bats, flying squirrels) and birds; also, some frogs and reptiles. Opportunistic and catholic in diet. In studies in Oregon, invertebrates formed 79-8% of food, with remaining 20-2% vertebrates; beetles accounted for 21-4% of diet, while grasshoppers and crickets (*Stenopelmatus*) comprised 52%; rodents of family Cricetidae made up 40-2% of vertebrate prey; likely that flexibility in habitat choice provides species with a fairly wide prey base. In winter in C Utah, diet consisted of 24-9% mammals, 51-3% birds and 23-8% insects; House Sparrow (*Passer domesticus*) the major component of most pellets. In Idaho, size range of prey mostly 16-35 g. Observed to take smaller and larger mice in inverse proportion to their availability, perhaps because smaller, younger prey more vulnerable or pose less risk of injury, or because energy expended in catching and killing large prey not worth risking. Nocturnal; somewhat crepuscular, foraging within 45 minutes after sunset. A sit-and-wait hunter, dropping from perch on to prey; will pursue prey over short distances; often catches bats in flight; also observed foraging on ground for earthworms.

Breeding. From Feb/Mar, earlier in S. Nest in natural tree cavity or old woodpecker hole, e.g. of flicker (*Colaptes*), sometimes in nest of Black-billed Magpie (*Pica pica*), or in cavity in cliff; also in juniper along dry streambeds; in giant saguaro, at heights from 1-2 m above ground almost to top; also uses nestboxes, 3-7 eggs, usually 4-6, with slight trend towards reduced clutch size from interior towards Pacific coast; laying interval 1-2 days; incubation c. 26 days, by female; chick with whitish down, brooded and fed by female, later fed by both parents; young leave nest at c. 28 days of age, tended by parents for further 5-6 weeks before independent.

Movements. Most populations resident; partial migrant in N. Juveniles may disperse longer distances to find unoccupied territory; in SW Idaho in Jun-Aug, c. 58 days after fledging.

Status and Conservation. Not globally threatened. CITES II. Fairly common to locally common. In many areas, has suffered substantial habitat losses with development of riparian woodland; however, relatively abundant food has allowed species to become more numerous in city parks and suburban areas. In Washington, individual found drowned, suspended in river from monofilament fishing line.

Bibliography. Abelow & Hardy (1997), Armstrong (1983), Baicich & Harrison (1997), Barrows (1989), Belthoff & Duffy (1995, 1998), Brown *et al.* (1986), Campbell *et al.* (1990), Dorn & Dorn (1994), Duffy & Belthoff (1997), Eckert (1974), Elliston & Orrell (1996), Ellsworth & Belthoff (1995a, 1995b), Feusier (1989), Fitton (1993), Hayward (1983), Hayward & Garton (1988), Heintzelman (1992), Holt & Hillis (1987), Howell & Webb (1995a), Johnsgard (1988), Kast (1998), Kaufman (1996), Levad (1989), Marks (1983), Marks & Marks (1981), Marti, Steenhof *et al.* (1993), Rawinski & Ryder (1991), Root (1988), Ross (1969), Small (1994), Smith & Wilson (1971), Stotz *et al.* (1996), Tyler & Phillips (1978), Voous (1988), Walker (1993), Walters (1983), Wolfe & de la Torre (1990).

43. Balsas Screech-owl

Otus seductus

French: Petit-duc du Balsas **German:** Balsaskreischeule **Spanish:** Autillo del Balsas

Taxonomy. *Otus vinaceus seductus* R. T. Moore, 1941, Michoacan, Mexico.

Sometimes considered to form superspecies with *O. kennicottii*, *O. cooperi* and *O. asio*. Often treated as race of *O. asio* or *O. kennicottii*, but differs in eye colour and vocalizations. Birds from Colima sometimes separated as race *colimensis*. Monotypic.

Distribution. SW Mexico, from S Jalisco and Colima to W Guerrero.



Descriptive notes. 24-26 cm; c. 155-165 g. Similar to race *vinaceus* of *O. kennicottii*; differs in larger size, browner ground colour above (still with pinkish wash), brown eyes (reported rarely as golden-brown), greenish bill; toes with large bristles; no rufous morph. Voice. Like bouncing-ball song of *O. kennicottii* but gruffer, "hooh-hooh-huh-huh-huhuhurr", soon repeated; also rather harsh whinnying scream.

Habitat. Arid open to semi-open areas, deciduous woodland with giant cardon, mesquite, thorn forest, tall cactus and second growth. From c. 600 m to 1500 m.

Food and Feeding. Little known. Insects and small vertebrates have been recorded.

Breeding. Lays during Jun; nest and eggs undescribed.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Described as fairly common to common, but little information available on status and ecology. Has been recently recorded between Autlán and Ciudad Guzmán (Jalisco), and at La Cumbre (Colima), Cañón de Lobos (Morelos) and Sierra de Atoyac (Guerrero). Available habitat appears to be decreasing. Currently being considered as candidate for inclusion in Red Data Book.

Bibliography. Anon. (1998a), Howell & Webb (1995a), Morris & Buffa (1996), Stotz *et al.* (1996).

44. Pacific Screech-owl

Otus cooperi

French: Petit-duc de Cooper **German:** Mangroveeule **Spanish:** Autillo de Manglar
Other common names: Oaxaca Screech-owl (*lambi*)

Taxonomy. *Scops cooperi* Ridgway, 1878, Santa Ana, Costa Rica.

Sometimes considered to form superspecies with *O. kennicottii*, *O. seductus* and *O. asio*. Often treated as race of *O. asio* or *O. kennicottii*, but appears to be vocally distinct from both. Race *lambi* proposed as full species, but latest studies indicate that subspecific treatment more appropriate: *chiapiensis* poorly differentiated, possibly not tenable. Three subspecies recognized.

Subspecies and Distribution.

- O. c. lambi* R. T. Moore & Marshall, 1952 - S Mexico (Pacific slope of Oaxaca).
- O. c. chiapiensis* R. T. Moore, 1947 - SE Mexico (Chiapas).
- O. c. cooperi* (Ridgway, 1878) - extreme SE Mexico (S Chiapas) to NW Costa Rica (Guanacaste).



Descriptive notes. 20-25.5 cm; 145-170 g (*cooperi*), c. 125 g (*lambi*). Facial disc pale grey with faint dusky rings, bordered by white mixed with dark brown; shaft markings on head narrow, so that crown appears no darker than back; rather pale tawny-grey above, finely vermiculated with dusky and with black shaft streaks; whitish scapular spots forming pale line, wing-coverts variably edged whitish; flight-feathers barred; off-white below, vermiculated with dusky and brown, with very narrow long black shaft streaks; tarsus fully feathered, toes bristly; iris yellow; bill greenish or with creamy-yellow tip. Juvenile greyish-buff above, whitish

below with deep buff on breast, with fine dusky barring. Race *lambi* smaller, more prominently dark crown contrasting with "frosty" areas around hindneck and face. Voice. Primary (secondary?) song up to 15 short notes rapidly delivered in series which rises in pitch at middle, then drops again, sometimes with initial short trill, "u-pu-pu-pu-pu...", or "prrr pu-pu-PU-PU-pu-pu"; also single, low gruff "woof" or "whuh"; *lambi* said to have whinnying secondary song.

Habitat. Dry woodland, semi-open country with scattered trees and bushes, palms and giant cardon and cactus, second growth and lakeside fields; also swamp-forest and edges of mangroves. Sea-level to 1000 m.

Food and Feeding. Mostly large insects, such as beetles, katydids, moths; also scorpions, and almost certainly small vertebrates (e.g. rodents).

Breeding. In Oaxaca, nest with 2 young and 1 egg in Mar, juvenile seen in May; presumably breeds mainly in dry season, around Mar. Nest in tree cavity or old woodpecker hole. 3-5 eggs; family group remains together into early wet season.

Movements. Resident, but little known.

Status and Conservation. Not globally threatened. CITES II. Considered fairly common to common in most of range, but no information on population size. Occurs in a series of protected areas in Costa Rica, including Santa Rosa, Palo Verde and Barra Honda National Parks.

Bibliography. Anon. (1998a), Binford (1989), Cooper (1997), Howell & Webb (1995a), Monroe (1968), Ridgely & Gwynne (1989), Slud (1964), Stiles & Skutch (1989), Stotz *et al.* (1996), Thurber *et al.* (1987).

45. Eastern Screech-owl

Otus asio

French: Petit-duc maculé

German: Ostkreischeule

Spanish: Autillo Yanqui

Other common names: Common Screech-owl

Taxonomy. *Strix Asio* Linnaeus, 1758, South Carolina.

Sometimes considered to form superspecies with *O. kennicottii*, *O. seductus* and *O. cooperi*. Formerly treated as conspecific with *O. kennicottii*, and may interbreed in areas of range overlap (separated by 60 km in Oklahoma "panhandle", slightly sympatric in Colorado Springs, broadly overlapping in Texas, undetermined in Mexico), but vocal and DNA analyses indicate that treatment as separate species more appropriate. Often considered to include *O. seductus* and *O. cooperi* as races. Geographical limits of listed races require further study; *naevius* sometimes merged with nominate. Additional described races probably reflect individual variation or intermediates only: *swenki* of SC Canada to Oklahoma included in *maxwelliae*; *semplei* from C Mexico in *mccallii*. Six subspecies recognized.

Subspecies and Distribution.

O. a. maxwelliae (Ridgway, 1877) - SC Canada and NC USA.

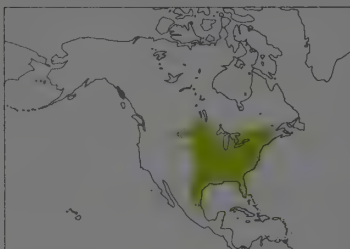
O. a. naevius (J. F. Gmelin, 1788) - SE Canada and NE USA (S to North Carolina).

O. a. asio (Linnaeus, 1758) - Oklahoma E to South Carolina and Georgia.

O. a. hasbroucki Ridgway, 1914 - C Oklahoma to Texas.

O. a. floridanus (Ridgway, 1874) - Louisiana to Florida.

O. a. mccallii (Cassin, 1854) - S Texas to NE Mexico.



Descriptive notes. 16-25 cm; male 166 g, female 194 g. Extremely similar to *O. kennicottii*; differs in more prominent, blackish rim to facial disc, somewhat less coarsely patterned underparts, and pale grey-green or dull green-blue (not blackish) bill; also, rufous morph more common, mainly in S, and more bright "foxy" in colour, with all grey or brown replaced by bright cinnamon-rufous or chestnut-rufous, upperparts without vermiculations, blackish streaks narrower and linear, underpart pattern less intricate. Juvenile grey to brownish-grey (grey morph) or dull rusty-red (rufous morph), face uniformly coloured, ear-

tufts inconspicuous and unicoloured (adult tufts bicoloured), faint barring on head, mantle and underparts. Races show degree of clinal variation, tend to become smaller and darker from N & W to S & E: *naevius* largest, much white below; *maxwelliae* pale above, whitish below, rare red morph very pale; *hasbroucki* with broad flank barring; *floridanus* with red morph predominant, dark rusty-brown above, light rufescent below; *mccallii* much more heavily mottled than other races. VOICE. Primary song quavering, low-pitched descending trill, c. 4-6-8-8 notes/second, ending abruptly, repeated after few seconds; also whinnying secondary song; female higher-pitched, duets.

Habitat. Tree-dominated landscapes: early successional to mature, mountain slopes to river valleys, below 1500 m. Occurs in natural woodland and wooded suburban and urban habitats, e.g. deciduous and mixed forest, riparian and pine forest; oak-juniper (*Quercus-Juniperus*) and subtropical thorn woodland in S; urban and suburban parks and gardens. Where overlaps with *O. kennicottii* in Texas, found along permanent watercourses and at lower elevation, with latter species inhabiting seasonally wet upland drainage areas. Prefers open subcanopy space with sparse shrub cover that facilitates flying and foraging, and perhaps predator detection.

Food and Feeding. Diet among most varied of any Nearctic owl: terrestrial and aquatic invertebrates (primarily insects, crayfish, earthworms), and wide range of vertebrates (especially songbirds, rodents). Most hunting nocturnal, but often crepuscular, occasionally diurnal. Perches below tree canopy, makes straight perch-to-prey strike, captures with feet; rarely flycatches with bill. Can take prey hidden in leaf litter; catches fish and tadpoles in water less than 10 cm deep, feet-first, flying from perch or hopping from shore; hovers, and flushes quarry with wingbeats. Walks, runs and hops on ground after prey; chicks do same on leaving nest. Kills or disables prey on ground or perch, by biting and tugging on head and neck; birds partially plucked; with vertebrates, usually eats head before caching body.

Breeding. Season Mar-Sept. Monogamous, occasionally polygynous. Nest-site a deep cavity with small entrance and large floor (hollow trunk, stump or limb, or hole in same), c. 30% old holes of woodpeckers (Picidae), most the result of storm damage to tree, or naturally rotted and/or enlarged by squirrels; in one study, most frequent trees used were pear (*Pyrus*), cottonwood (*Populus*), oak (*Quercus*), elm (*Ulmus*) and pine (*Pinus*); artificial sites include nestboxes, mailboxes, porch columns, discarded boxes on ground, dove-cotes. Usually 3-4 eggs, but up to 7; infertile eggs sometimes removed from cavity and replaced; sequential mate of polygynous male may displace earlier female and add to existing clutch; incubation at least 26 days, by female; chick hatches with eyes closed, egg tooth prominent, whitish down; fledging 25-27 days; fledglings dependent on parents for 8-10 weeks, stay together, mostly in tree roosts, and fed by both parents. Annual number fledglings/nesting pair 2-6 in Michigan; in Texas, 1-9 (suburban) and 1-0 (rural). Most breed as yearlings. First-year survival in Texas estimated at 36% (suburban) and 30% (rural). Maximum recorded age 14 years and 2 months; average only 1 year in female *hasbroucki*.

Movements. Resident; may make local or altitudinal movements in severe winters or during food shortages.

Status and Conservation. Not globally threatened. CITES II. Long-term effects of human impacts on species as a whole doubtful. Pesticide-related eggshell-thinning and embryo mortality not found in wild, but can be induced in laboratory experiments. Reducing tree density below c. 50 trees/ha or removing natural cavities leads to species's total disappearance; tree-planting in deforested or naturally grassy areas fosters population expansion, although nestboxes required when trees young; human settlement with tree-planting possibly advantageous. Patchy habitat and riparian corridors suggest that partly disjunct local populations are metapopulations, some stable parts of

which may be source of immigrants for others unable to maintain stability. Urbanization and climatic warming may promote range expansion to N; moderate climate, enhanced and concentrated food supplies, constant water sources, and reduced number of predators (factors common to urban and suburban environments) considered beneficial.

Bibliography. Abel & Ritchison (1995), Adam (1987, 1989), Atkins (1986), Baicich & Harrison (1997), Bakehouse (1986), Beatty (1988), Belthoff (1987), Belthoff & Duffy (1998), Belthoff & Ritchison (1989, 1990a, 1990b), Belthoff *et al.* (1993), Bosakowski & Smith (1997), Breen & Parrish (1996), Carpenter, T.W. (1987), Cavanagh & Ritchison (1987), Cinguina (1995), Clark (1983), Cook (1998), Curtler (1997), De Geus & Bowles (1990, 1991), Duguay *et al.* (1997), Eckert, A.W. (1974), Eckert, K.R. (1997), Ehrlich *et al.* (1992), Fragner (1995a), Gehlbach (1988, 1989, 1994a, 1994b, 1994c, 1995), Gehlbach & Baldrige (1987), Gehlbach & Leverett (1995), Gehlbach & Roberts (1997), Greer (1997), Heintzelman (1992), Hjertaas (1986), Holt *et al.* (1995), Houston (1989), Howell & Webb (1995a), Johnsgard (1979, 1988), Jorgensen (1988), Kast (1998), Kaufman (1996), Kaufman & Bowers (1989), Klatt (1992), Klatt & Ritchison (1993, 1994), Lawless *et al.* (1997), Loos & Kerlinger (1993), Lohrer (1985), Mazur (1992), Mosher & Henny (1976), Nero (1994b), Ritchison & Cavanagh (1992), Ritchison, Belthoff & Sparks (1992), Ritchison, Cavanagh *et al.* (1988), Root (1988), Rowley (1984), Schaldach (1963), Smith (1993), Smith & Hiestand (1990), Smith & Wiemeyer (1992), Smith *et al.* (1987), Sparks (1990), Sparks *et al.* (1994), Sproat (1992), Sproat & Ritchison (1993, 1994), Stewart (1989), Stewart & Tyler (1989), Stotz *et al.* (1996), Sutton (1986), Tyler & Phillips (1978), Urban (1959), Van Camp & Henny (1975), Voous (1988), Walker (1993), Weber (1990), Wiemeyer (1987), Wiemeyer & Hoffman (1996), Wolfe & de la Torre (1990).

46. Whiskered Screech-owl

Otus trichopsis

French: Petit-duc à moustaches

German: Fleckeneule

Spanish: Autillo Bigotudo

Other common names: Spotted Screech-owl, Whiskered Owl

Taxonomy. *Scops trichopsis* Wagler, 1832, Puebla, Mexico.

Relationships uncertain. Several additional races described: *pinosus* (Veracruz), *ridgwayi* (Michoacán) and *guerreroensis* (SW Mexico) included in nominate *trichopsis*; *pumilus* from Honduras in *mesamericanus*. Three subspecies recognized.

Subspecies and Distribution.

O. t. aspersus (Brewster, 1888) - SE Arizona to N Mexico (Sonora and Chihuahua).

O. t. trichopsis (Wagler, 1832) - highlands of C Mexico (from about Durango S to Veracruz, Oaxaca and Chiapas).

O. t. mesamericanus van Rossem, 1932 - SE Mexico (Chiapas) to NC Nicaragua.



Descriptive notes. c. 16-19 cm; male 70-105 g, female 80-120 g. Occurs in grey-brown and rufous morphs, latter more in S. Facial disc pale grey with faint dusky rings, area of deep brown immediately above eye, disc mostly bordered boldly with black; dark grey to brownish-grey above with blackish shaft streaks, scapulars with black-edged whitish to light buff outer webs; flight-feathers prominently barred pale; pale below, with dark vertical stripe down shaft of each feather, crossed by dark horizontal bars, streaks broadest on breast. Rufous morph with black streaks above, pale cinnamon-buff to light cinnamon-rufous

below with indistinct dusky bars on flanks. Tarsus fully feathered; iris yellow; bill grey. Juvenile duller above, with indistinct barring or transverse mottling, dull white underparts broadly barred grey-brown. Racial variation shows trend from NW to SW from grey through blackish to brown, from medium to coarse to fine markings, increase of rufous decoration of grey morph, and appearance of rufous morph in S: *aspersus* light grey; *mesamericanus* rufous-brown, with black dorsal cross-bars. VOICE. Primary song a series of c. 8 evenly spaced "boot" or "boo" notes, uniform in pitch or slight drop at end, lasting up to almost 3 seconds; secondary song 2 short and closely spaced notes, followed by 2-5 longer notes; female versions of both higher-pitched; calls include a "chang," a trill and a "shee".

Habitat. Occurs in dense groves of oaks within pine-oak zone of montane vegetation; prefers denser groves and higher elevations than *O. asio*. In Arizona and parts of Mexico, ranges down into dense oaks below pine zone; in S Mexico and El Salvador, also above pine forest to lower parts of cloudforest; also in El Salvador, occurs within coffee plantations, where it breeds in tall shade trees, occupying groves and thickets remaining after incomplete logging has opened up denser forest. From 750 m to c. 2500 m.

Food and Feeding. Primarily insects, usually winged; among favoured prey are grasshoppers (Acrididae, Tettigoniidae), beetles (*Phyllophaga*), moths (Phalaenidae, Zanolidae); centipedes (*Scopelendra*) evidently an important winter food, at least locally; stomach contents included a mouse. Nocturnal. Hunts from perch in tree, making short, straight flight to winged prey from an exposed branch; commonly flutters back and forth in tops of trees, catching insects in succession, with relatively little pause between captures; prey occasionally taken on ground, on dead branch of a neighbouring tree, or on vegetation.

Breeding. Eggs found in Apr and May. Few nests located, all in natural cavity or old hole of flicker (*Colaptes*), 5-5-6 m above ground in tree (recorded in oak, walnut, juniper and sycamore). 3-4 eggs; incubation by female; no other information.

Movements. Probably resident, occurring too far S to be significantly affected by winter reduction in insect populations; perhaps some vertical migration to lower elevations during winter, at least in N of range.

Status and Conservation. Not globally threatened. CITES II. Common to fairly common. Fire suppression in mountains of S Arizona, resulting in thickening of woodland and forest growth, may have increased its distribution at expense of *O. asio*; species will probably continue to abound wherever dense vegetation allowed to remain on steep N-facing mountainsides and in narrow, shady canyons. In Mexico, where naturally occurring fires not curbed, more open forest favours *O. asio* and *O. flammeolus*; logging further opens up growth, restricting species to dense stands remaining on steep slopes and in deep canyons. Overall, occupies any groves and pockets remaining after incomplete logging and in areas partly opened up for agriculture; in El Salvador, can live within coffee plantations, in artificial forest of tall shade trees. Population or trends little known, but clearly dependent on the future of fairly dense montane forest within its range.

Bibliography. Baicich & Harrison (1997), Binford (1989), Eckert (1997), Heintzelman (1992), Howell & Webb (1995a), Johnsgard (1988), Kaufman (1996), Kaufman & Bowers (1989), Land (1970), Ligon & Brenowitz (1976), Martin (1974), Monroe (1968), Ridgely & Gwynne (1989), Ross (1969), Rowley (1984), Schaldach (1963), Smith *et al.* (1982), Stotz *et al.* (1996), Tyler & Phillips (1978), Voous (1988), Wolfe & de la Torre (1990).

47. Tropical Screech-owl

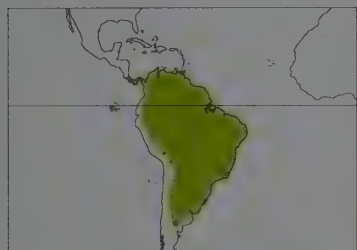
Otus choliba

French: Petit-duc choliba **German:** Cholibaeule **Spanish:** Autillo Chóliba
Other common names: Choliba Screech-owl

Taxonomy. *Strix choliba* Vieillot, 1817, Paraguay. Relationships unclear; appears to have no close affinities with any other *Otus*. Has in past included *O. koepckeae* and *O. roboratus* as races, but those both clearly distinct in morphology and/or vocalizations. Several additional races described, probably only morphs or result of individual variation: *montanus*, *kelsoi*, *alticola*, *cauca*, *guyanensis* and *portoricensis* included in *crucigerus*; *caatingensis* in *decussatus*; *chapadensis* in nominate *choliba*; *alilucoco* in *wetmorei*. Nine subspecies recognized.

Subspecies and Distribution.

O. c. luctisomus Bangs & Penard, 1921 - Costa Rica to NW Colombia, including Pearl Is.
O. c. margaritae Cory, 1915 - Margarita I, off N Venezuela.
O. c. choliba (Vieillot, 1817) - S Brazil (S Mato Grosso, São Paulo) to E Paraguay.
O. c. wetmorei Brodtkorb, 1937 - W Paraguay and N Argentina (S to Mendoza, N Buenos Aires and N Rio Negro).
O. c. uruguayensis Hekstra, 1982 - NE Argentina, SE Brazil (Santa Catarina, Rio Grande do Sul) and Uruguay.



Descriptive notes. 20-24 cm; 97-160 g. Occurs in grey-brown, brown and rufous morphs, with intermediates, and much individual variation; rufous morph scarce. Facial disc light grey with prominent broad black border; crown and upperparts heavily streaked dark, scapulars with dark-edged pale spots; flight-feathers and tail barred light buff and brown; underparts white, thinly vermiculated with brown and small amounts of buff, with black shaft streaks throughout, each feather with fishbone-like pattern; tarsus feathered, toes completely bare; iris yellow; bill greenish-grey with grey tip; feet grey-brown. Juvenile mostly buffy, finely

barred dusky, darker above. Races differ mainly in size, though minimal, and plumage differences difficult to assess owing to range of variation; *duidae* very dark, with pale collar on hindneck. Voice. Primary song a brief trill followed by 2, occasionally 1 or 3, louder toots. "prrrr pu POO, prrrr POO poo, prrrr p'p' poo"; sometimes trill or toots alone; secondary song bubbling "bububububu"; calls include strident screeching barks, "kwah-hwah-kwah".

Habitat. Timbered savanna, gallery forest, forest clearings and edge, and semi-open areas with scattered trees, second-growth thickets, plantations; also town and suburban parks. Generally from sea-level to c. 1500 m; in Costa Rica to 700 m; in Colombia to 2800 m, but sightings reported at up to 3000 m; in Argentina locally to 2700 m, but usually at lower levels; records at higher altitudes apparently dependent on favourable climatic conditions.

Food and Feeding. Mostly insects, especially large orthopterans such as grasshoppers and crickets, as well as scarabids, bumblebees, moths; also spiders and scorpions, earthworms; occasionally snakes (*Helminthophis*), and sometimes small mammals such as rats (*Oryzomys*); bats also taken. Forages at lower levels, usually from perch, often along roadside; captures prey on branches or on ground; often snatches insects in air, especially at electric lights.

Breeding. Lays Jan-Jul, regularly May; Sept-Oct in S. Nest in any kind of cavity, natural or old woodpecker hole; also uses abandoned boxes. Usually 1-4 eggs, but 6 reported in Argentina; incubation by female; chick with whitish down; in Costa Rica, young left nest when 30 days old (in Mar).

Movements. Little known; probably resident.

Status and Conservation. Not globally threatened. CITES II. Widely distributed and rather common; most common screech-owl in Costa Rica and Panama; fairly common in Brazil, Argentina and Uruguay. Little is known, however, about its population levels and ecology. Habit of hunting along roadsides makes it vulnerable to traffic; mortality on roads quite high in some places. Some local human persecution.

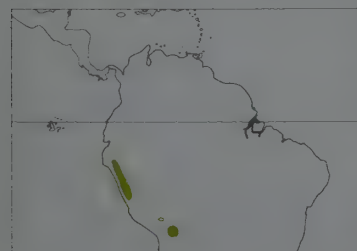
Bibliography. Belton (1984), Browning (1990), Canevari *et al.* (1991), Contreras (1983), Contreras *et al.* (1990), Fjeldså & Krabbe (1990), Haverschmidt & Mees (1994), Herklots (1961), Hilty & Brown (1986), Klimaitis & Moschione (1987), König (1994b), Meyer de Schauensee & Phelps (1978), Monroe (1968), Olrog (1985), de la Peña (1994), Piacentini & Acebo (1998), Ridgely & Gwynne (1989), do Rosário (1996), Saibene *et al.* (1996), Short (1975), Sick (1993, 1997), Slud (1964), Snyder (1966), Stiles & Skutch (1989), Stotz *et al.* (1996), Thomas (1977), Tostain *et al.* (1992), Wetmore (1968a).

48. Koepcke's Screech-owl

Otus koepckeae

French: Petit-duc de Koepcke **German:** Andenkreischeule **Spanish:** Autillo de Koepcke
Other common names: Maria Koepcke's Screech-owl

Taxonomy. *Otus choliba koepckeae* Hekstra, 1982, Cordillera Blanca, Peru.



Originally described as race of *O. choliba*, but distinctly different in morphology; taxonomy requires further study to clarify true relationships. Species name sometimes incorrectly spelt *koepcke*. Monotypic.

Distribution. NW Peru (probably from around Amazonas, and Ancash S to Lima, possibly farther S, to Ayacucho or beyond); apparently also WC Bolivia (to La Paz). Distributional limits very imperfectly known.

Descriptive notes. c. 24 cm; c. 110-120 g. Resembles *O. roboratus*; differs in larger size, paler crown and forehead, less obvious nuchal collar, broader and more prominent shaft

streaks below, light ochre-brown wash across neck sides and breast. Juvenile unknown. Voice. Not described.

Habitat. Wooded areas and arid forest patches on Andean slopes, up to *Polylepis* woodland, in upper montane zone at 2500-4500 m.

Food and Feeding. No information. Probably insects.

Breeding. No information.

Movements. No information.

Status and Conservation. Not globally threatened. CITES II. Very poorly known; no information on numerical status, ecology or biology. Warrants classification as Data-deficient.

Bibliography. Fjeldså & Krabbe (1990), Hekstra (1982b), Stotz *et al.* (1996).

49. Peruvian Screech-owl

Otus roboratus

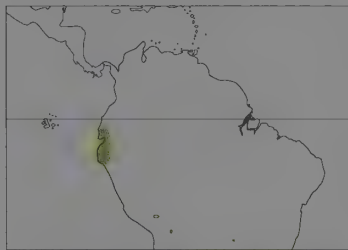
French: Petit-duc du Pérou **German:** Buscheule **Spanish:** Autillo Peruano
Other common names: West Peruvian/Roborate Screech-owl; Coastal/Tumbes Screech-owl (*pacificus*)

Taxonomy. *Otus roboratus* Bangs and Noble, 1918, Bellavista, Peru.

Has been treated as conspecific with *O. choliba*, but vocalizations distinct. Smaller race *pacificus* suggested as possibly separate species; further study needed. Two subspecies recognized.

Subspecies and Distribution.

O. r. pacificus Hekstra, 1982 - SW Ecuador and extreme NW Peru (S to Lambayeque).
O. r. roboratus Bangs & Noble, 1918 - extreme S Ecuador and NW Peru between W & C Andes (drainage of R Chinchipe and R Marañón).



Descriptive notes. c. 20-22 cm, 144-162 g (*roboratus*); c. 70-90 g (*pacificus*). Occurs in grey-brown and rufous morphs. Facial disc greyish-white, narrowly barred dusky, with black border; small ear-tufts grey-white and warm brown; crown blackish-brown, giving capped effect, contrasting strongly with white eyebrows; distinct pale nuchal collar; upperparts grey-brown, slightly barred dark, with blackish shaft streaks; inner wing with narrow cinnamon-brown bars and dusky speckles; scapulars with black-edged whitish outer webs; flight-feathers barred buffy-white; underparts whitish, faintly vermiculated, with variable but

often fine dark shaft streaks with lateral bars, central belly often clear white; tarsus fully feathered; iris yellow to golden; bill grey with yellow tip; feet greyish. Rufous morph pale rufous with dark brown markings. Juvenile densely barred, iris pale yellow-olive. Race *pacificus* smaller, less heavy, averages paler and greyer but much overlap; rufous morph commoner than in nominate. Voice. Typical song a harsh, rising trill, marginally increasing in frequency towards end, lasting c. 2-5 seconds; *pacificus* said to give rapid series of notes, rising in volume in middle, dropping slightly and then fading, c. 1-5 seconds long; in aggression, series of short upward-inflected yelps, and from *pacificus* downslurred "kii".

Habitat. Dry deciduous woodland with scattered bushes on mountain slopes and in hilly country, mostly at 500-1200 m, occasionally higher. Race *pacificus* inhabits arid coastal plains and foothills, generally below 500 m; habitats range from open, dry scrub of various shrubs, cacti, mesquite and various short trees, to dry deciduous forest of small to medium-sized trees and columnar cactus (*Cereus*); other typical species include *Capparis*, *Acacia*, *Prosopis* and *Bombax*.

Food and Feeding. Largely insectivorous, perhaps almost exclusively so; known to take caterpillars, orthopterans, grasshoppers, crickets, and beetles and their larvae. Nocturnal.

Breeding. Nest in cavity of moderate-sized tree; no other information.

Movements. Probably resident.

Status and Conservation. Not globally threatened. CITES II. Can be very common locally, but overall rare and possibly vulnerable; both N and S limits of distribution, however, uncertain. Since early 1970's, much habitat rendered unsuitable by effects of grazing by goats, and by cutting of trees and shrubs for firewood and for charcoal production; although able to occupy very sparse woodland and scrub, at least for foraging, and probably to lesser extent for roosting, species may not be able to survive in such open habitat without trees of at least moderate stature that can provide nesting cavities. Because of pastoral economy typical of region, goat browsing and firewood-gathering difficult to control; however, harvesting for charcoal could be discouraged wherever possible.

Bibliography. Best & Kessler (1995), Best *et al.* (1993), Cook (1996), Fjeldså & Krabbe (1990), Johnson & Jones (1985, 1990), Koepcke (1970), Meyer de Schauensee (1982), Olrog (1968), Parker *et al.* (1982), Pople *et al.* (1997), Stotz *et al.* (1996), Taylor (1995), Williams & Tobias (1996), Williams *et al.* (1996).

50. Bare-shanked Screech-owl

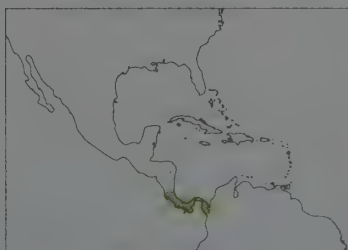
Otus clarkii

French: Petit-duc de Clark **German:** Nacktbeineule **Spanish:** Autillo Serrano

Taxonomy. *Otus clarkii* L. Kelso and E. H. Kelso, 1935, Calobre, Panama.

Relationships unknown. Monotypic.

Distribution. Costa Rica S to extreme NW Colombia.



Descriptive notes. 20-25 cm; 125-180 g. Large screech-owl with large head, ear-tufts smaller than most other *Otus*. Face cinnamon with poorly defined facial rim; rufous-brown above, spotted blackish, hindneck more buff, scapulars with blackish-edged outer webs; flight-feathers barred; underparts darkish, throat and breast buffy-brown with buff-white spots and black streaks, belly with more white; only upper two-thirds of tarsus feathered, lower section and toes bare; iris yellow; bill grey; lower tarsus and toes greyish-flesh. Juvenile cinnamon-buff above, speckled with white and barred dusky, buffy-white below with dull cinnamon bars.

VOICE. Primary song a deep "wook wook wook", repeated at intervals of few seconds; secondary

song deep whistled "hu-hu, HOO-HOO hoo", penultimate note usually highest; female songs slightly higher-pitched, often in duet; call rather high, musical, hooting "coo, coo-coo-coo".

Habitat. Cloudforest and humid, dense mountain forest and forest edge; sometimes occurs in thinner upland forest. From 900 m to c. 2350 m, occasionally to 3300 m.

Food and Feeding. Mainly large insects, including crickets, grasshoppers and beetles, also spiders; some shrews and small rodents also taken. Hunts at dusk and at night, along edges, in clearings and sometimes in canopy. Prey normally captured on ground or on branches; observed to take insects close to artificial lights.

Breeding. Little known. Lays mid Feb-May; fledged young seen May-Aug. Only known nest was in natural cavity in oak (*Quercus copeyensis*).

Movements. Presumably resident.

Status and Conservation. Not globally threatened, CITES II. Restricted-range species: present in Costa Rica in several protected areas, such as Volcán Poás National Park and Monteverde Biological Reserve, and occurs in Panama Highlands EBA and Darién Highlands EBA. Considered uncommon; little known about population level. Needs at least patchy forest; in Costa Rica, habitat adversely affected by development of dairy industry. With restricted distribution in mountains in Middle America, and possible threats to habitat, conservation status of species should probably be reassessed.

Bibliography. Anon. (1998a), Hilty & Brown (1986), Olog (1968), Ridgely & Gwynne (1989), Robbins *et al.* (1985), Slud (1964), Stattersfield *et al.* (1998), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968a).

51. Bearded Screech-owl

Otus barbarus

French: Petit-duc bridé

German: Tropfeneule

Spanish: Autillo Barbudo

Other common names: Bridled/Santa Barbara Screech-owl

Taxonomy. *Scops barbarus* P. L. Slater and Salvin, 1868, Santa Barbara, Vera Paz, Guatemala. Relationships uncertain; has been considered ecological counterpart of *O. flammeolus*. Monotypic.

Distribution. Highlands of S Mexico (Chiapas) and N Guatemala.



Descriptive notes. 16-20 cm; c. 70 g. Small screech-owl with very small ear-tufts; wings project beyond short tail. Occurs in brown and rufous morphs. Pale facial disc with thin dark border; spotted with brown, white and black above, white spots heavier on upper mantle, scapulars with black-edged whitish outer webs; flight-feathers strongly barred; breast densely barred brown and buff, fading to white with light barring on flanks and belly, with dark shaft streaks throughout; tarsus feathered; iris yellow; bill greenish-grey; toes pinkish-grey. Rufous morph less patterned, dark markings more reddish-brown. Juvenile barred. **VOICE.**

Short fast trill of 3-5 seconds' duration, increasing in volume, at times dropping abruptly at end; also soft ventriloquial "hu".

Habitat. Highland pine and pine-oak forest, and cloudforest, from 1400 m to 2500 m above sea-level, mostly above 1800 m.

Food and Feeding. Mainly large insects.

Breeding. Nest undescribed; 4-5 eggs; no other information.

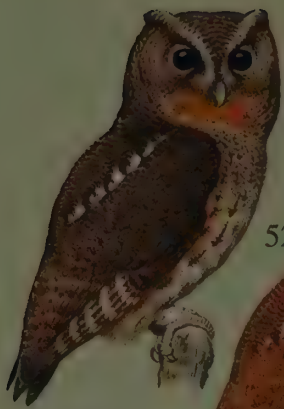
Movements. Resident.

Status and Conservation. Not globally threatened, CITES II. Restricted-range species: present in North Central American Highlands EBA. Currently considered Near-threatened. Considered fairly common but very local. Population level unknown, but possibly decreasing. In Chiapas, habitat apparently becoming fragmented. Requires research on its biology and ecology in order for true conservation status to be assessed.

Bibliography. Anon. (1998a), Hernández-Baños *et al.* (1995), Howell & Webb (1995a), Land (1970), Stattersfield *et al.* (1998), Stotz *et al.* (1996).

PLATE 9

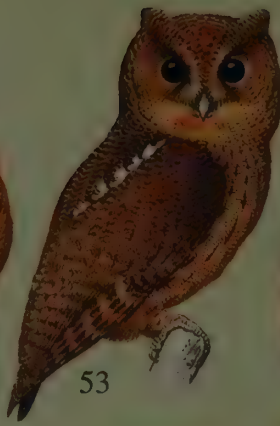
inches 5
cm 13



brown morph



rufous morph



brown morph



rufous morph



ssp usta
rufous morph

56



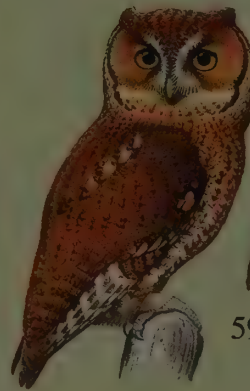
rufous morph



brown morph



rufous morph



rufous morph



brown morph



ssp nudipes



ssp newtoni



rufous morph



brown morph



rufous morph



brown morph



68



64



65



66



67



52. Rufescent Screech-owl

Otus ingens

French: Petit-duc de Salvin **German:** Salvineule **Spanish:** Autillo Pálido
Other common names: Salvin's Screech-owl; Chapman's Screech-owl ("*aequatorialis*"); Least Screech-owl ("*minimus*")

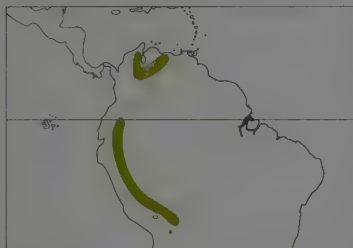
Taxonomy. *Scops ingens* Salvin, 1897, Jima, Ecuador.

Relationships uncertain. Often considered to include *O. colombianus* as race; *O. petersoni* treated as conspecific by some authors. Forms described from E Ecuador (*aequatorialis*) and Bolivia (*minimus*) now thought to represent individual variation, synonymized with nominate. Two subspecies recognized.

Subspecies and Distribution.

O. i. venezuelanus Phelps & Phelps, Jr., 1954 - N Colombia and NW Venezuela.

O. i. ingens (Salvin, 1897) - Andes from NE Ecuador to WC Bolivia.



Descriptive notes. 24-28 cm; male 134-180 g, female 140-223 g. Large, rather uniform-looking screech-owl with vestigial ear-tufts, large brown eyes. Occurs in brown and rufous morphs. Facial disc buffy-brown, with indistinct rings and weakly defined border, usually with pale (but not white) eyebrows; upperparts tawny-olive to light grey-brown, or sandy-rufous, with fine dark vermiculations, few whitish spots, and whitish scapular line; underparts light buffish-white, finely barred light brown and white, with a few widely spaced dark brown streaks; tarsus fully feathered; iris brown; bill olive to yellow-grey; toes yellowish.

grey to pink. Juvenile with dense dusky mottling, also indistinct mask. Race *venezuelanus* slightly smaller, paler than nominate. **Voice.** Primary song a long rapid series of "tu" notes, c. 50 in 10 seconds; secondary song an almost even-pitched series suddenly accelerating after c. 4 notes, "hu hu hu hu tutututu".

Habitat. Dense, humid cloudforest and scrub on steep Andean slopes, at 1200-2250 m.

Food and Feeding. Poorly known; presumed to take primarily insects. Strictly nocturnal. Apparently forages in middle storey and canopy.

Breeding. No reliable information.

Movements. Probably resident.

Status and Conservation. Not globally threatened. CITES II. Status is uncertain, and species little known; may be rare, unless overlooked. Occurs in at least two protected areas in Colombia, i.e. La Planada and Río Nambi National Reserves. Forest destruction probably a threat in some parts of range. Conservation status in need of review.

Bibliography. Fitzpatrick & O'Neill (1986), Fjeldså & Krabbe (1990), Fjeldså & Mayer (1996), Hilty & Brown (1986), Meyer de Schauensee & Phelps (1978), Olrog (1968), Stotz *et al.* (1996), Wetmore (1968b).

53. Colombian Screech-owl

Otus colombianus

French: Petit-duc de Colombie **German:** Kolumbieneule **Spanish:** Autillo Colombiano

Taxonomy. *Otus colombianus* Traylor, 1952, El Tambo, 5000 feet [c. 1700 m], Cauca, Colombia. Often treated as race of *O. ingens*. Sometimes *O. petersoni* treated as race of present species. Monotypic.

Distribution. W slope of Andes from WC Colombia to NW Ecuador.



Descriptive notes. 26-28 cm; male 150-156 g, female c. 210 g. Occurs in grey-brown and rufous morphs. Very similar to *O. ingens*; differs in having longer tarsus which is also bare distally; scapular stripe often less distinct, more buffish; flight-feathers and underparts without white. **Voice.** Much as *O. ingens*; whether vocally distinct from latter still debated.

Habitat. Cloudforest with dense understorey, at c. 1300-2300 m.

Food and Feeding. Large insects and small vertebrates.

Breeding. No reliable information.

Movements. Probably resident.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Chocó EBA. Currently considered Near-threatened. Status uncertain, and species little known; may be rare. Forest destruction probably a threat, at least locally. Conservation status perhaps in need of review.

Bibliography. Fitzpatrick & O'Neill (1986), Fjeldså & Krabbe (1990), Hilty (1997), Hilty & Brown (1986), Kirwan & Marlow (1996), Olrog (1968), Stattersfield *et al.* (1998), Stotz *et al.* (1996).

54. Cinnamon Screech-owl

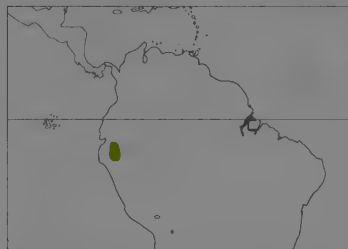
Otus petersoni

French: Petit-duc de Peterson **German:** Zimtkreiseule **Spanish:** Autillo de Peterson

Taxonomy. *Otus petersoni* Fitzpatrick and O'Neill, 1986, Cordillera del Cóndor, Peru.

Possibly forms superspecies with *O. marshalli*; both formerly included under invalid name *O. huberi*. Alternatively, considered by some to be conspecific with *O. ingens* or *O. colombianus*. Scientific name sometimes incorrectly spelt as *petersenii*. Monotypic.

Distribution. Cordillera del Cutucú in SE Ecuador S to La Peca region in NW Peru.



Descriptive notes. c. 21 cm; male 88-119 g, female 92-105 g. Relatively small, with medium-length ear-tufts. Entire plumage warm buff-brown to cinnamon-brown; facial disc with lighter chin and eyebrows, indistinct darker rim; upperparts finely vermiculated, scapulars with light cinnamon outer webs; flight-feathers and tail barred; underparts slightly paler than upperparts, more cinnamon, with darker shaft streaks; tarsus feathered almost to toes; iris dark brown; bill greenish-grey; toes pinkish. Distinguished from *O. colombianus* by smaller size, deeper cinnamon coloration, more extensive tarsal feathering. Juvenile undescribed. **Voice.** Presumed primary song a rapid series of simple notes, c. 5-7 per second, rising slightly and then dropping, and ending abruptly, whole phrase c. 5-6 seconds long; also "wew" calls.

Habitat. Cloudforest with dense undergrowth, rich in epiphytes and mosses, at c. 1700-2500 m.

Food and Feeding. Mainly insects; probably some small vertebrates.

Breeding. Season probably May-Jun; no other information.

Movements. Probably resident.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Ecuador-Peru East Andes EBA. Very poorly known, and no information on numbers; described as probably rare. Destruction of forest habitat probably a long-term threat. Conservation status in need of revision.

Bibliography. Clark & Mikkola (1989), Fitzpatrick & O'Neill (1986), Fjeldså & Krabbe (1990), Rahbek *et al.* (1995), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Taylor (1995), Williams *et al.* (1996), Vuilleumier *et al.* (1992).

55. Cloudforest Screech-owl

Otus marshalli

French: Petit-duc de Marshall **German:** Nebelwald-Kreiseule **Spanish:** Autillo de Marshall

Taxonomy. *Otus marshalli* Weske and Terborgh, 1981, Cordillera Vilcabamba, 2180 m, Cuzco, Peru. Possibly forms superspecies with *O. marshalli*; both formerly included under invalid name *O. huberi*. Monotypic.

Distribution. C & S Peru in Pasco (Cordillera Yanachaga) and Cuzco (Cordillera Vilcabamba).



Descriptive notes. 20-23 cm; c. 115 g. Rather small, with short ear-tufts. Facial disc rufous, border black at sides, with white eyebrows; crown and upperparts rich rufous-brown, with transverse pattern of blackish mottling, and buffy nuchal collar; scapulars with blackish-tipped buffy to whitish outer webs; flight-feathers and tail barred; breast rufous with dark shaft streaks and thin vermiculations; lower breast and belly off-white with dark streaks and thin cross-bars, appearing almost "ocellated"; tarsus fully feathered; iris dark brown; bill greenish-grey; toes flesh-pink. Differs from *O. ingens* in smaller size, more strongly patterned

underparts. Juvenile much as adult. **Voice.** Presumed primary song a rather fast, regular series of "ii" notes, phrase c. 5-10 seconds long, repeated after short interval.

Habitat. Humid, mossy cloud forest with epiphytes, ferns and dense undergrowth, generally at 1900-2500 m, possibly higher; occurs at slightly higher elevations than *O. ingens*.

Food and Feeding. Probably insectivorous; forages in canopy; needs further study.

Breeding. Little information. Appears to breed in late Jun-Aug, sometimes earlier; male collected in early Mar was not in breeding condition.

Movements. Probably resident.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Peruvian East Andean Foothills EBA. Poorly known; thought to be not uncommon locally, but no indication of numbers. Destruction of forest habitat probably a long-term threat. Conservation status perhaps in need of revision.

Bibliography. Clark & Mikkola (1989), Fitzpatrick & O'Neill (1986), Fjeldså & Krabbe (1990), Parker *et al.* (1982), Schulenberg *et al.* (1984), Shuker (1993), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Vuilleumier *et al.* (1992), Weske & Terborgh (1981).

56. Tawny-bellied Screech-owl

Otus watsonii

French: Petit-duc de Watson **German:** Watsoneule **Spanish:** Autillo del Amazonas
Other common names: Austral/Southern Screech-owl (*usta*)

Taxonomy. *Ephialtes Watsonii* Cassin, 1848, Orinoco River, Venezuela.

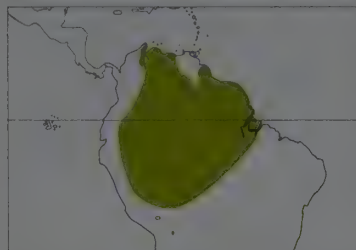
Suggested to belong to the *O. atricapillus* superspecies, but large overlap in range with *O. vermiculatus*. From vocal evidence and DNA sequencing appears closest to *O. atricapillus*; more distantly related to *O. choliba* than previously thought. Race *usta* has been treated as separate species; compared with nominate, however, differences in morphology appear to be minimal and vocal dissimilarities probably not constant; also, their ranges may partly overlap. Two subspecies recognized.

Subspecies and Distribution.

O. w. watsonii (Cassin, 1848) - lowlands from E Colombia S to NE Peru and E (N of R Amazon) to Surinam and Amazonian Brazil.

On following pages: 57. Guatemalan Screech-owl (*Otus guatemalae*); 58. Vermiculated Screech-owl (*Otus vermiculatus*); 59. Hoy's Screech-owl (*Otus hoyi*); 60. Variable Screech-owl (*Otus atricapillus*); 61. Long-tufted Screech-owl (*Otus sanctaecatarinae*); 62. Puerto Rican Screech-owl (*Otus nudipes*); 63. White-throated Screech-owl (*Otus albugularis*); 64. Palau Owl (*Pyrroglaux podarginus*); 65. Cuban Screech-owl (*Gymnoglaux lawrencii*); 66. Northern White-faced Owl (*Ptilopsis leucotis*); 67. Southern White-faced Owl (*Ptilopsis granti*); 68. Giant Scops-owl (*Mimizukura gurneyi*).

O. w. usta (P. L. Sclater, 1859) - E Peru and S Amazonian Brazil S to lowland forest of N Bolivia and N Mato Grosso.



Descriptive notes. 19-24 cm; c. 115-155 g. Facial disc and eyebrows brown-buff, with faint blackish vermiculations and thin dark border; longish, broad ear-tufts with black outer webs and tips; crown and upperparts dark grey-brown, spotted and vermiculated with black and buff, hint of buff on hindneck; scapular spots indistinct or lacking; flight-feathers and tail barred brown and light buff; breast dark brown with small buff spots; rest of underparts buff, streaked with black, with obscure white barring on belly; tarsus fully feathered buff; iris brownish-orange to yellow; bill green-grey; toes yellow-brown to pinkish-grey. Juvenile undescribed. Race *usta*

similar in pattern, but slightly smaller, rufous overall, broader streaks below; also occurs in browner and buffer morphs. **Voice.** Primary song soft, low and full, beginning with monotonous "whooh" notes, becoming faster and louder, then fading with low trill, phrase c. 20 seconds long; secondary song brief series of short "wu" notes. Race *usta* primary song similar, c. 2 notes per second; secondary song thought to be fast series of "bu" notes, slowing to "bouncing" rhythm at end.

Habitat. Interior of lowland rainforest, especially old-growth primary forest and mature second growth; occasionally in clearings or at edge; *usta* also inhabits remnant forest along rivers. Lives in lower storey of forest, usually found no more than 30 m above the ground, often descending into undergrowth. Generally at elevations not exceeding c. 600 m.

Food and Feeding. Mostly insects; probably also terrestrial vertebrates. Forages in the lower levels. **Breeding.** No information.

Movements. Presumably resident.

Status and Conservation. Not globally threatened. CITES II. Status uncertain, and species poorly known. Since it seems to be restricted to forest, the major threat to its survival must surely be destruction of its habitat. Nominate race occurs in several protected areas, such as Amacayacu National Park in Leticia, Colombia, and Imataca Forest Reserve in Bolívar, Venezuela. Conservation status in need of revision.

Bibliography. Blake (1962), Fitzpatrick & O'Neill (1986), Friedmann (1948), Haverschmidt & Mees (1994), Heidrich *et al.* (1995b), Hekstra (1982a), Hilty & Brown (1986), Kirwan & Sharpe (1999), König (1994b), Meyer de Schauensee & Phelps (1978), Olrog (1968), Robinson & Terborgh (1997), Sargeant (1994a), Schmitt *et al.* (1986), Sick (1993, 1997), da Silva *et al.* (1997), Stotz, Fitzpatrick *et al.* (1996), Stotz, Lanyon *et al.* (1997), Tostain *et al.* (1992), Willard *et al.* (1991).

57. Guatemalan Screech-owl

Otus guatemalae

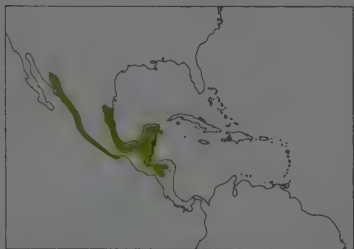
French: Petit-duc guatémalteque **German:** Rotgesichteule **Spanish:** Autillo Guatemalteco
Other common names: Middle American Screech-owl

Taxonomy. *Scops guatemalae* Sharpe, 1875, Guatemala.

Perhaps a member of a superspecies, along with *O. vermiculatus*, *O. hoyi*, *O. atricapillus* and *O. sanctaecatarinae*. Sometimes considered conspecific with *O. atricapillus*; has been treated as conspecific with *O. vermiculatus*, but vocally distinct. Races *tomlini*, *fuscus* and *thompsoni* possibly inadequately differentiated to merit subspecific status; proposed races *pettingilli* and *peteni* included in *hastatus* and nominate *guatemalae* respectively. Seven subspecies recognized.

Subspecies and Distribution.

- O. g. tomlini* R. T. Moore, 1937 - NW Mexico (S Sonora and SW Chihuahua S to Sinaloa).
- O. g. hastatus* (Ridgway, 1887) - SW Sinaloa to Oaxaca.
- O. g. cassini* (Ridgway, 1878) - E Mexico (S Tamaulipas and N Veracruz).
- O. g. fuscus* R. T. Moore & J. L. Peters, 1939 - Veracruz.
- O. g. thompsoni* Cole, 1906 - Yucatán Peninsula and Cozumel I.
- O. g. guatemalae* (Sharpe, 1875) - SE Mexico (S Veracruz and NE Oaxaca) to Honduras.
- O. g. dacrysiactacus* R. T. Moore & J. L. Peters, 1939 - N Nicaragua.



Descriptive notes. 20-23 cm; 100-150 g. Occurs in brown and rufous morphs. Brown morph with facial disc light brown and lightly barred white, with thin dark border, thin white eyebrows contrasting with short dark ear-tufts; indistinct pale nuchal collar; crown heavily spotted and barred blackish; upperparts relatively dark grey-brown to blackish-brown with darker vermiculations and streaks, scapulars with black-edged whitish outer webs; flight-feathers and tail barred; paler below, with blackish shaft streaks and vermiculations, strongest on breast; tarsus fully feathered; iris yellow; bill greenish-grey; toes flesh-coloured. Rufous morph less

boldly patterned. Differs from *O. vermiculatus* in feathered lower tarsus, stronger markings. Juvenile similar to adult, faintly barred. Races differ in tone of coloration and in size, which increases from N to SE: *cassini* smallest, also darkest; *dacrysiactacus* pale; *hastatus* intermediate. **Voice.** Primary territorial song a quavering trill, c. 14 notes per second, increasing in pitch and volume, ending abruptly, usually 6-15 but up to 20 seconds in duration; secondary song short series of notes, speeding up in bouncing-ball rhythm.

Habitat. Humid lowland to semi-arid evergreen forest, semi-deciduous forest and thorn forest; also dense second growth and similar scrub and plantations. From sea-level to 1500 m.

Food and Feeding. Mainly large insects, such as beetles, katydids, orthopterans; also frogs, reptiles and fish; sometimes rodents. Nocturnal hunter, using forest clearings and edge. Hunts from perch, swooping on to prey on ground or branch; also catches insects in flight.

Breeding. Lays mostly Mar-Apr, but incubation recorded in Jun in Yucatán Peninsula; juveniles observed in Jun. Nest in cavity of tree, often old woodpecker hole; recorded in old nest of trogon (*Trogon*). 3 eggs (2-5); incubation by female.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Little information available; appears to be not rare locally. Has been recorded at San Blas (Nayarit), El Sumidero and Bonampak (Chiapas) and Cobá and Felipe Carrillo Puerto (Quintana Roo). Populations have probably declined as a result of forest destruction. Habitat loss a threat, at least in long term.

Bibliography. Anon. (1998a), Binford (1989), Heidrich *et al.* (1995b), Howell & Webb (1995a), König (1991a), Land (1970), Monroe (1968), Ridgely & Gwynne (1989), Schaldach (1963), Sutton & Pettingill (1942), Stiles & Skutch (1989), Stotz *et al.* (1996), Voous (1988).

58. Vermiculated Screech-owl

Otus vermiculatus

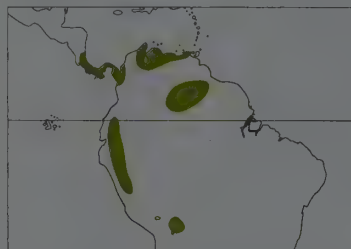
French: Petit-duc vermiculé **German:** Bänderkreischeule **Spanish:** Autillo Vermiculado

Taxonomy. *Megascops vermiculatus* Ridgway, 1887, Costa Rica.

Perhaps a member of a superspecies, along with *O. guatemalae*, *O. hoyi*, *O. atricapillus* and *O. sanctaecatarinae*. Sometimes considered conspecific with *O. guatemalae*, but vocally distinct. Isolated races *roraimae* and *napensis* possibly separate species; further study needed. Additional races described from Peru (*helleri*) and Bolivia (*bolivianus*) here merged with *napensis*, but possibly merit subspecific recognition. Three subspecies recognized.

Subspecies and Distribution.

- O. v. vermiculatus* (Ridgway, 1887) - NE Costa Rica to NW Colombia, N Venezuela.
- O. v. roraimae* (Salvin, 1897) - S Venezuela and N Brazil (mountain regions of Roraima, Duida and Neblina).
- O. v. napensis* Chapman, 1928 - E Ecuador to Peru, and N Bolivia.



Descriptive notes. 20-23 cm; c. 100-110 g. Occurs in brown and rufous morphs. Brown morph with facial disc light brown with thin dark rings, indistinct border, pale eyebrows obscure; greyish-brown to buffy-brown above, finely and uniformly vermiculated with black; scapulars with white outer webs; flight-feathers prominently barred; whitish below, densely and finely vermiculated with black and brown, with some dark shaft streaks; tarsus feathered almost to toes; iris deep yellow; bill grey-green; toes pinkish-grey. Rufous morph bright uniform rufous above and on head. Distinguished from *O. guatemalae* by bare lower

tarsus, less strongly patterned plumage. Juvenile dull buffy-brown, abdomen and flanks with down feathers tipped greyish-white. Race *roraimae* darker, more heavily patterned; *napensis* with distinct white eyebrows, sometimes brown eyes. **Voice.** Primary song very fast, long, toad-like trill, starting softly, becoming louder, then dropping in pitch and fading out towards end; female may answer with shorter, higher trill; probable secondary song a very brief descending purr; also "ghoor" or "khoo" calls. Races *roraimae* and *napensis* similar to *O. guatemalae*, but song shorter.

Habitat. Humid tropical forest in lowlands and foothills, to c. 1200 m. Race *roraimae* inhabits rainforest on mountain slopes, at 1000-1800 m; *napensis* mostly above 250 m, up to 1500 m.

Food and Feeding. Mainly large insects; probably also some small vertebrates.

Breeding. Lays during Mar in N. Nest in natural tree cavity or old nest hole of other bird. 3 eggs. **Movements.** Resident.

Status and Conservation. Not globally threatened. CITES II. Needs almost solid forest. Very little information; possibly not rare locally. Has been recorded at Finca La Selva, on the Caribbean lowlands of Costa Rica, and the Pipeline road, in central Panama. Forest destruction a threat, at least in long term.

Bibliography. Chapman (1931), Heidrich *et al.* (1995b), Hilty & Brown (1986), König (1994b), Marín & Schmitt (1991), Meyer de Schauensee & Phelps (1978), Ridgely & Gwynne (1989), Sargeant (1994a), Sick (1993, 1997), Slud (1960, 1964), Stiles & Skutch (1989), Stotz *et al.* (1996), Voous (1988), Wetmore (1968a), van der Weyden (1974), Willis & Eisenmann (1979).

59. Hoy's Screech-owl

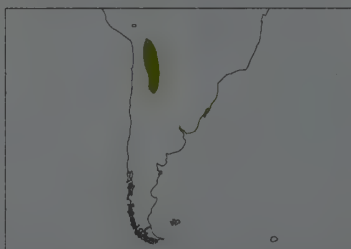
Otus hoyi

French: Petit-duc de Hoy **German:** Hoyeule **Spanish:** Autillo Fresco
Other common names: Montane Forest Screech-owl

Taxonomy. *Otus hoyi* König and Straneck, 1989, mountain forest at La Cornisa, c. 40 km north of the city of Salta, Argentina.

Perhaps a member of a superspecies, along with *O. guatemalae*, *O. vermiculatus*, *O. atricapillus* and *O. sanctaecatarinae*. Sometimes considered conspecific with *O. atricapillus*, but vocally distinct, and treatment as separate species supported by DNA evidence. Monotypic.

Distribution. Mountains of S Bolivia (S from Cochabamba) and NW Argentina (S to Tucumán, possibly to Catamarca).



Descriptive notes. 24 cm; 115-145 g. Occurs in grey, brown and rufous morphs. Facial disc grey-brown with fine, dark markings and white eyebrows, bordered in black; upperparts with dark vermiculations and streaks; small half-circle of white feathering at back of head; scapulars with long row of big white spots, many divided by a dark stripe; flight-feathers barred, tail with light brown stripes and vermiculations; underside light grey to grey-brown, washed with ochre-brown; breast and flanks with strong black shaft streaks; tarsus fully feathered grey-brown; iris bright deep yellow; bill yellow-green; toes grey-brown to

flesh. Grey morph distinctly grey-tinged, rufous morph rusty. Differs from grey morph of *O. chotiba* in less marked dark rim around facial disc, presence of white semi-circle on back of head, less bold markings. **Voice.** Primary song begins softly, gradually swells into rapid staccato of "u" notes, 11 per second, and tapers off at end; phrase c. 8 seconds, followed by pause of variable length according to intensity of vocal activity, then begins again; female higher-pitched, less full; pair duets; secondary song similar but short, ends abruptly, in excitement, loud long rising notes.

Habitat. Montane forest and cloudforest, in more or less moist areas with tall, thick trees and epiphytes; in SE Salta (Argentina), found only a few km from dry brush and trees in closed forest. Occurs at 1000-2600 m, locally to 2800 m.

Food and Feeding. Primarily insectivorous.

Breeding. Probably lays in Sept-Oct; in one study, main singing activity noted in last third of Sept; breeding probably dependent on onset of heavier rainfall, with subsequent flush of insects. Nest mainly in old woodpecker cavity; in one study, species found only in forest areas with such cavities, and pair occupied old hole of woodpecker 7 m above ground. No information on clutch size and other details.

Movements. Probably resident; some altitudinal movement to lower levels likely in winter.

Status and Conservation. Not globally threatened. CITES II. Appears not uncommon locally. Probably subject to some loss of habitat through deforestation, perhaps also overgrazing; will occupy forest patches on slopes where felling more difficult, which may aid future survival. Present in a number of protected areas in Argentina, such as El Rey National Park, Salta, and species is to some extent protected by the inaccessibility of parts of its range.

Bibliography. Babarskas *et al.* (1995), Canevari *et al.* (1991), Chebez (1994), Fjeldså & Mayer (1996), Heidrich *et al.* (1995b), Herzog *et al.* (1997), König (1991a, 1994b), König & Straneck (1989), Krabbe *et al.* (1996), Kratter *et al.* (1993), Mazar *et al.* (1997), Stotz *et al.* (1996), Straneck, Ridgely & Rodríguez (1987), Vuilleumier *et al.* (1992).

60. Variable Screech-owl

Otus atricapillus

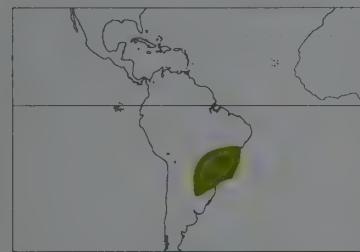
French: Petit-duc à mèches noires **German:** Kappeneule **Spanish:** Autillo Capirotado
Other common names: Black-capped Screech-owl

Taxonomy. *Strix atricapilla* Temminck, 1822, Brazil.

Perhaps a member of a superspecies, along with *O. guatemalae*, *O. vermiculatus*, *O. hoyi* and *O. sanctaecatarinae*. Sometimes considered to include some or most of those as races, but all now shown to be vocally distinct, and treatment as separate species supported by DNA evidence. Southern populations have been sometimes separated as *argentinus*. Taxonomy of *Otus* in S Brazil and Argentine province of Misiones remains to be clarified. Monotypic.

Distribution. SE Brazil (S Bahia and Goiás S to Santa Catarina), SE Paraguay and extreme NE Argentina (N Misiones).

Descriptive notes. 23-24 cm; c. 115-140 g. Occurs in grey, brown and rufous morphs. Resembles *O. guatemalae*; differs in larger ear-tufts, darker crown, lighter facial disc with more distinct dark border, bolder streaks below, dark brown eyes; in grey and rufous morphs, iris sometimes dark golden-yellow or yellow-brown. Juvenile undescribed. **Voice.** Primary song a long fast trill, very faint before increasing in volume, ending abruptly, phrase 8-14 seconds, sometimes up to 20 seconds, repeated after some seconds; secondary song short, c. 2.5-3 seconds, in bouncing-ball rhythm; female higher-



pitched, primary song shorter; duets.

Habitat. Humid forest, especially extensive rainforest; partial to thick vine forest with dense undergrowth, and forest edge; occasionally more open woodland, sometimes near villages and roads. Mainly in lowlands, to at least 600 m in N of range; generally lower in S, to 300 m in Argentina.

Food and Feeding. Primarily insects, including beetles, locusts, cicadas and moths; probably also some small vertebrates. Forages in canopy, but frequently lower down, among undergrowth; takes prey from foliage, branches or the ground.

Breeding. 3 males with enlarged testes in Oct and Nov. Solitary, territorial, but at times almost semi-colonial, appears to breed in close proximity to conspecifics. Nest in tree cavity, including old woodpecker holes. No other details.

Movements. Probably resident.

Status and Conservation. Not globally threatened. CITES II. May be locally fairly common; in Argentina, found to be locally common in N Misiones in 1950's, and possibly still common in e.g. Iguazú National Park. Currently considered uncommon to locally fairly common in Paraguay. Occurs in Aparados da Serra National Park, Rio Grande do Sul, but no data on population levels in Brazil. Species should be monitored because of the scale of habitat loss in its range; it seems to require fairly large areas of forest, and may not be able to survive in small remnant forest reserves.

Bibliography. Brooks *et al.* (1993), Canevari *et al.* (1991), Hayes & Scharf (1995b), Heidrich *et al.* (1995b), Hekstra (1982a), König (1991a, 1994b), Lowen, Barnett *et al.* (1997), Pacheco *et al.* (1996), do Rosário (1996), Saibene *et al.* (1996), Sick (1993, 1997), Stotz *et al.* (1996).

61. Long-tufted Screech-owl

Otus sanctaecatarinae

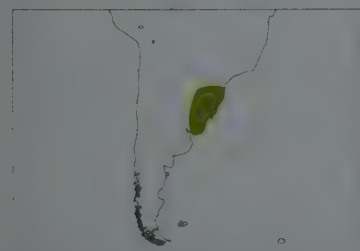
French: Petit-duc à aigrettes longues **Spanish:** Autillo de Santa Catarina
German: Langohr-Kreischeule

Taxonomy. *Scops sanctae-catarinae* Salvin, 1897, southern Brazil.

Perhaps a member of a superspecies, along with *O. guatemalae*, *O. vermiculatus*, *O. hoyi* and *O. atricapillus*. Formerly considered conspecific with *O. atricapillus*, but vocally and morphologically distinct, and treatment as separate species further supported by DNA evidence. Taxonomy of *Otus* in S Brazil and Argentine province of Misiones remains to be clarified. Monotypic.

Distribution. SE Brazil (Paraná, Santa Catarina, Rio Grande do Sul), NE Argentina (Misiones) and Uruguay.

Descriptive notes. 24-27 cm; male 155-194 g, female 174-211 g. Large *Otus*, with heavy body and strong feet. Occurs in brown and rufous morphs. Resembles *O. atricapillus*; differs in larger size and bulkier build, long and wider ear-tufts, lighter-coloured crown, usually less distinct streaking, yellow eyes (rarely light brown), much stronger feet and talons. Juvenile undescribed. **Voice.** Male primary song a fast trill, c. 13-14 notes per second, similar to *O. guatemalae* but louder, lower and slower, and may slightly ascend or descend or move to rougher notes, lasts 6-10 seconds, ends suddenly;



female version shorter, higher; male secondary song short fast notes that become longer and more spaced, in reversed bouncing-ball rhythm, phrase c. 5 seconds; female secondary song loud, hoarse, extraordinary, "bababa...", unlike any other screech-owl.

Habitat. Semi-open woodland, wooded pasture, upland moors with patches of *Araucaria*, and forest edge and secondary growth; locally, trees and copses in and near villages and agricultural areas; avoids dense forest. Found mainly at 300-1000 m.

Food and Feeding. Insects and small vertebrates. Reported as a sit-and-wait hunter, dropping from perch on to prey.

Breeding. Season apparently from late Aug/Sept; nest in tree cavity; no other information.

Movements. Probably resident.

Status and Conservation. Not globally threatened. CITES II. Common in forested parts of Rio Grande do Sul and Santa Catarina; formerly locally common in N Misiones, in NE Argentina, but appears to have declined. Generally overlooked, especially as a result of confusion with *O. atricapillus*. Loss of habitat through overgrazing, burning and tree-felling represents greatest threat to species.

Bibliography. Belton (1984), Chebez (1994), Heidrich *et al.* (1995b), Hekstra (1982a), König (1991a, 1994b), Olog (1968, 1984, 1985), de la Peña (1994), Sick (1993, 1997), Stotz *et al.* (1996).

62. Puerto Rican Screech-owl

Otus nudipes

French: Petit-duc de Porto Rico **German:** Nacktfußeule **Spanish:** Autillo Portorriqueño
Other common names: Puerto Rican Bare-legged Owl; Virgin Islands Screech-owl, Newton's Owl (*newtoni*)

Taxonomy. *Strix nudipes* Daudin, 1800, Puerto Rico.

Earlier suggestion that it may form superspecies with Cuban *Gymnoglaux lawrencii* considered unacceptable; latter separated at generic level by very different morphology and vocal patterns. Validity of race *newtoni* has been disputed, possibly only a morph. Two subspecies recognized.

Subspecies and Distribution.

O. n. nudipes (Daudin, 1800) - Puerto Rico.

O. n. newtoni (Lawrence, 1860) - Vieques 1 off E Puerto Rico (1 record, probably extinct), and unconfirmed report from nearby Culebra I; also Virgin Is (St Thomas, St John, Tortola, Virgin Gorda, St Croix, probably Guana I).



Descriptive notes. 23-25 cm; c. 100-150 g. Medium-sized, with markedly rounded head lacking ear-tufts. Occurs in brown and rufous morphs. Facial disc rather dark, with whitish eyebrows, lores and chin, and faint dark border; upperparts with light spots and irregular narrow dark bars, scapulars with variable white on outer webs; wings and tail barred; underparts paler, with numerous darker vermiculations and shaft streaks, becoming whitish and less patterned on belly; upper tarsus feathered, lower bare; iris orange-brown; bill greenish-yellow; lower tarsus and toes yellow. Rufous morph less patterned. Juvenile nearly uniform

olive-brown above, head and neck lighter brown, underparts distinctly barred dusky brown and pale fulvous. Race *newtoni* rufous-tinged, less patterned below. **Voice.** Primary song short, deep trill c. 3-5 seconds long; secondary song shorter, 2 seconds, slight rise in middle, then dropping and fading out; female higher-pitched; also cackling and cooing calls.

Habitat. Forest and woodland of all types; coffee plantations, isolated coastal thickets, also small thickets and groves of large trees in urban areas; roosts in caves, trees and dense foliage by day. Sea-level to 900 m.

Food and Feeding. Mainly insects, such as grasshoppers and crickets; occasional small vertebrates. Emerges at night to hunt.

Breeding. Season Apr-Jun. Nest in tree cavity or cave, sometimes in cliff crevice. Usually 2 eggs (1-4); incubation by female; chick with whitish down.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Puerto Rico and the Virgin Islands EBA. Common in Puerto Rico, with no immediate threats obvious. Race *newtoni* extremely rare, possibly extinct: only 1 report ever from Vieques, considered possibly unreliable; no proof that species ever existed on Culebra; on St Croix, no verified records since 19th century; on St Thomas and St John, no definite 20th-century records, although unverified sightings by residents reported from St Thomas; despite historical reports from Guana, Tortola and Virgin Gorda, no verified records traced for any of those islands; some claims of this species known to have referred to misidentified *Asio flammeus*. In survey of Virgin Is in 1995, using playback of song recordings, no owls heard or seen. Race *newtoni* seems always to have been rather rare; destruction of forest for plantation crops, mainly since middle of 19th century, no doubt hastened its decline.

Bibliography. Anon. (1998a), Biaggi (1983), Bond (1985), Clark & Mikkola (1989), Gannon *et al.* (1993), Gundlach (1873), King (1978/79), Leck (1975), Lembeke (1850), Moreno (1998), Nellis (1979), Pardieck *et al.* (1992, 1996), Raffaele (1989), Raffaele *et al.* (1998), Rivera-Milan (1995), Stattersfield *et al.* (1998), Stotz *et al.* (1996), van der Weyden (1974), Wiley (1985, 1986a, 1986b).

63. White-throated Screech-owl

Otus albugularis

French: Petit-duc à gorge blanche **German:** Weißkehleule **Spanish:** Autillo Gorgiblanco

Taxonomy. *Syrnium albugularis*, Cassin, 1849, Choachi, Bogotá.

Sometimes placed in monotypic genus *Macabura*, or that name used as subgenus, on basis of lack of erectile ear-tufts. Vocal patterns, however, show close relationship with New World *Otus*. Races *obscurus* and *aequatorialis* possibly only morphs, or result of individual variation. Six subspecies recognized.

Subspecies and Distribution.

O. a. obscurus Phelps & Phelps, Jr., 1953 - Sierra de Perijá, in NW Venezuela.

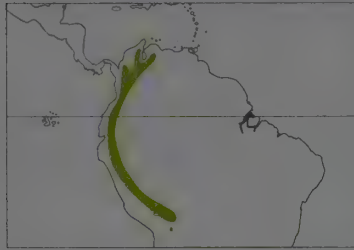
O. a. meridensis (Chapman, 1923) - Andes of W Venezuela.

O. a. macabrum (Bonaparte, 1850) - C & W Andes from Colombia and Ecuador S to N Peru.

O. a. albogularis (Cassin, 1849) - E Andes of Colombia and N Ecuador.

O. a. aequatorialis (Chapman, 1922) - E Ecuador.

O. a. remotus Bond & Meyer de Schauensee, 1941 - E Andes from Peru S to C Bolivia (Cochabamba).



greyish; toes pinkish-grey. Juvenile pale buffy-grey, with orbital discs and long bristles above bill forming black mask, barred crown, mantle and underparts; on fledging resemble adult, but pattern more obscure. Race *meridensis* with whitish forehead and eyebrows, numerous pale freckles on upperparts suggesting nuchal collar; other races darker; *remotus* darkest, blackish above with few white and rufous spots, dark breast contrasting with poorly marked lower underparts. Voice. Male song 7-30 gruff, barked notes, "churrochurro-churro-chu chu chu chu", can be given uninterruptedly for 1 minute, possibly primary song; also evenly spaced hoots, c. 5 per second, gradually dropping, also reported as descending trill of 10-14 hoots every 5-10 seconds, probably secondary song; often, both sexes sing in more or less synchronized duet, female slightly higher-pitched; also gives single hoots.

Habitat. Humid montane evergreen forest, especially stunted alpine forest; mostly open forest and edge, and semi-open areas with scattered trees; habitat often rich in epiphytes and bamboo thickets, sometimes with glades or at least gaps in canopy. Occurs mostly at 2000-3000 m, but locally down to 1300 m.

Food and Feeding. Poorly known. Mainly insects; some small vertebrates. Nocturnal; forages in canopy.

Breeding. Female with enlarged ovary in Jul in Peru; nestlings in Oct in Ecuador; juveniles in Jan in Ecuador, Mar in C Peru, Sept in Venezuela. Nest possibly on ground in ferns and grass; or in old nest of other bird in tree or bush, e.g. incubated egg found in deserted cup nest above ground; probably also in natural holes when available. No other information.

Movements. Probably resident; likely to make seasonal altitudinal movements.

Status and Conservation. Not globally threatened. CITES II. Poorly known, but perhaps often overlooked; probably common; in surveys within known range, seen or heard in small numbers (fewer than 10 individuals) on daily basis. Has been recorded recently in Páramo de Tamá (Venezuela), at Río Blanco (Colombia), and along Baeza-Tena road (Ecuador) and Cuzco-Manu road (Peru). Conservation priority considered low to medium.

Bibliography. Baez *et al.* (1997), Fjeldså & Krabbe (1990), Hilty & Brown (1986), Koeppke (1961), Krabbe *et al.* (1997), Meyer de Schauensee & Phelps (1978), Olrog (1968), Stotz *et al.* (1996).

Genus *PYROGLAUX* Yamashina, 1938

64. Palau Owl

Pyrroglaux podarginus

French: Petit-duc des Palau

German: Palauleule

Spanish: Autillo de las Palau

Other common names: Palau Scops-owl

Taxonomy. *Noctua podargina* Hartlaub and Finsch, 1872, Palau Islands.

Often placed in *Otus*, but appears to be more distantly related to that genus. Monotypic.

Distribution. Palau Is (Babelthup, Koror, Peleliu and Angaur).



joins in duet, with lower, mellower song. The calls are not dissimilar to notes uttered by the Palau Fruit-dove (*Ptilinopus felewensis*), which can also be heard at night.

Habitat. All types of forest; frequently found in middle and upper levels of woodland trees and lagoon trees; often in deep ravines, and mangrove swamps; also steep forested ridges; noted near villages.

Food and Feeding. Large orthopterans and centipedes, arthropods and earthworms.

Breeding. Lays Feb-Mar. Territorial, in pairs and family groups throughout year; territory 100-200 m in diameter; nest in hollow tree. No other information.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Palau EBA. Current status uncertain. Formerly said to be abundant throughout its tiny range, with territories very densely spaced; in mid 1940's, 33 pairs found on Koror and 4 on Peleliu; has apparently declined since then. Further field research required to determine present population level.

Bibliography. Baker (1951), Clark & Mikkola (1989), Engbring (1988), Marshall (1949), Mayr (1945), Pratt, Bruner & Berrett (1987), Pratt, Engbring *et al.* (1980), Stattersfield *et al.* (1998).

Descriptive notes. 22 cm. Dark reddish-brown owl with large, rounded head without ear-tufts; facial disc only marginally paler, with whitish lores and eyebrows; upperparts with few light streaks, scapulars with black-tipped white spots; lighter below, with some pale barring and spotting; tarsus bare; iris brown; bill white; legs and feet whitish. Juvenile barred on crown, back and underparts. Voice. Male song a long series of low, mellow "whok" notes which rise in intensity and pitch to a sharp, whistled "quirt-quirt" or "wut-who", latter repeated at 2-second intervals in flight, faster with increasing excitement; female commonly

Genus *GYMNOGLAUX* Cabanis, 1855

65. Cuban Screech-owl

Gymnoglaux lawrencii

French: Petit-duc de Cuba

German: Kubaeule

Spanish: Autillo Cubano

Other common names: Bare-legged Owl/Screech-owl

Taxonomy. *Gymnoglaux lawrencii* P. L. Sclater and Salvin, 1868, Remedios, Cuba.

Often placed in *Otus*. Earlier suggestion that it may form superspecies with Puerto Rican *Otus nudipes* considered unacceptable; separated from latter at generic level by very different morphology and vocal patterns. Possibly related to *Athene*. Race *exsul* often not recognized. Two subspecies recognized.

Subspecies and Distribution.

G. l. exsul (Bangs, 1913) - W Cuba and I of Pines.

G. l. lawrencii P. L. Sclater & Salvin, 1868 - C & E Cuba.



Descriptive notes. 20-23 cm. Rather small, with large head lacking ear-tufts. Facial disc creamy-white with broad dark rim, long white eyebrows; upperparts brown, occasionally rufous-brown, spotted with white and black; wings barred; relatively long tail with only 10 feathers; creamy below, washed buff on breast, with dark shaft streaks; tarsus bare; iris brown; bill yellowish-grey; legs and feet yellow. Rather like *Athene cunicularia*, but underparts whiter, streaked. Juvenile sienna above and on breast, shading to lighter on belly. Race *exsul* very like nominate.

VOICE. Male song a low, accelerating "cu-cu-cu-cucuk" in bouncing-ball rhythm, rising slightly at end, also repeated "cu co, cu co, cu co..."; female utters harsh shriek, "hui hui hui hui ...".

Habitat. Wooded areas, mixed forest of palm, tropical semi-deciduous forest, and thickets; also large plantations.

Food and Feeding. Mainly large insects, but also frogs, snakes and, rarely, birds.

Breeding. Season Jan-Jun. Nest in tree cavity, including old woodpecker holes, sometimes in cave or sheltered cliff crevice. 2 eggs; chick with whitish down. Record of pair living more than 7 years in same area.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Considered fairly common or common, and widely distributed; rare on Cayo Romano and Cayo Coco, and probably also on Guajaba and on Sabinal Peninsula. Not well known, however, and more information needed on species' ecology and exact status.

Bibliography. Anon. (1998a), Barbour (1943), Bond (1985), Criado *et al.* (1995), Jiménez (1997), Raffaele *et al.* (1998), Stotz *et al.* (1996), Sulley & Sulley (1992), Wotzkow (1990).

Genus *PTILOPSIS* Kaup, 1851

66. Northern White-faced Owl

Ptilopsis leucotis

French: Petit-duc à face blanche de Temminck

German: Nordbüscheleule

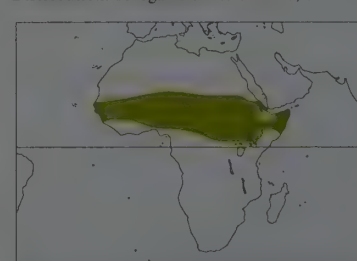
Spanish: Autillo Cariblanco Norteño

Other common names: White-faced Scops-owl/Owl (with *P. granti*)

Taxonomy. *Strix leucotis* Temminck, 1820, Senegal.

Genus until recently merged with *Otus*, but shown by molecular-biological studies to be very different, and eyes also much bigger. Often treated as conspecific with *P. granti*; significant differences in DNA and vocal patterns, however, indicate that N and S populations specifically distinct. Pale birds in Sudan and dark ones elsewhere have been treated as racially distinct (as *margarethae* and *nigrovertex*, respectively), but both considered merely colour morphs. Monotypic.

Distribution. Senegambia E to Somalia, S to N Zaire, N Uganda and C Kenya.



Descriptive notes. c. 25 cm; wingspan 50 cm. Facial disc off-white, outlined in black; crown and nape light grey with dark grey vermiculations; long ear-tufts edged in black; upperparts pale grey to grey-brown, faintly vermiculated, with darker grey streaks, contrasting white scapular line; flight-feathers and tail grey-brown, barred with light grey; greyish-white below, with thin dark grey streaks and fine vermiculations; iris deep yellow to orange; bill creamy-horn; toes greyish. Dark morph darker, with brownish tinge, crown almost black; rare light morph very pale. Distinguished from *P. granti* by paler upperparts, yellow eyes. Ju-

venile paler and browner, head and breast not so heavily marked, facial disc pale grey, eyes yellow; also no ear-tufts and shorter tail. Voice. Mellow "po proo", repeated at intervals of 4-8 seconds; also low "ta-wit-ta-weet" in contact.

Habitat. Savanna and dry woodland with sparse ground cover, semi-desert with scattered thorn trees and wooded desert watercourses, to dense woodland with closed canopy; also forest edge and clearings; often near settlements, even in suburban gardens and towns in W. From sea-level to 1700 m.

Food and Feeding. Small mammals; also some birds, and insects including moths, beetles, spiders and scorpions. At 1 nest, 85% of prey small mammals, 10% arthropods, 5% birds. Requires c. 25 g

food/day. Nocturnal and crepuscular hunter. Hunts from perch, including telegraph wires, and drops on to prey by flapping and gliding low over ground; sometimes hunts around street lights; swallows prey whole, rarely plucking larger birds.

Breeding. Lays Jan-Sept; in Ghana said to breed Oct-Jan. Monogamous; solitary, but sometimes several pairs within 200 m of each other, and larger clutches, when food abundant. Nest small to large stick platform of other bird, such as pigeon (Columbidae), turaco (*Tauraco*), eagle or hawk (Accipitridae) or heron (Ardeidae), sometimes cavity or crevice in tree, usually 2-8 m above ground. 2-3 (1-4) eggs; incubation from first egg, by female, occasionally by male briefly, period c. 30 days; chick with whitish down; young brooded by female, male delivers food; young climb around outside nest at c. 27 days, can fly well at 30-32 days, remain with parents for at least 2 more weeks.

Movements. Resident; possibly some short-distance movements depending on rains and prey abundance.

Status and Conservation. Not globally threatened. CITES II. Locally common to uncommon throughout its range; less common and more local in E of range; rare resident in Somalia, only 11 confirmed records. Occurs in a number of protected areas throughout its range, such as Abuko Nature Reserve in Gambia, W National Park in Niger, Ouadi Rimé Reserve in Chad and Bamingui-Bangoran and Manovo-Gounda-Saint Floris National Parks in Central African Republic.

Bibliography. Ash & Miskell (1983b, 1998), Bannerman (1953), Barlow *et al.* (1997), Britton (1980), Cave & Macdonald (1955), Cheke & Walsh (1996), Colston & Curry-Lindahl (1986), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Elgood *et al.* (1994), Field (1998), Fry *et al.* (1988), Gatter (1997), Giraudoux *et al.* (1988), Gore (1990), Grimes (1987), Kemp & Kemp (1998), Lewis & Pomeroy (1989), Mackworth-Praed & Grant (1957, 1970), Marshall, I. (1997), Short *et al.* (1990), Snow, D.W. (1978, 1979), Steyn (1984), Zimmerman, D.A. *et al.* (1996).

67. Southern White-faced Owl

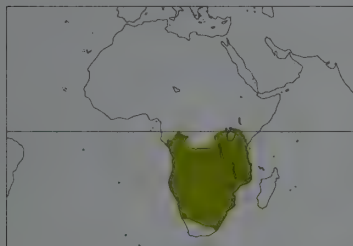
Ptilopsis granti

French: Petit-duc de Grant **German:** Südbütscheule **Spanish:** Autillo Cariblanco Sureño
Other common names: White-faced Scops-owl/Owl (with *P. leucotis*)

Taxonomy. *Pisorhina leucotis granti* Kolliway, 1910, Namibia.

Genus until recently merged with *Otus*, but shown by molecular-biological studies to be very different, and eyes also much bigger. Often treated as conspecific with *P. leucotis*, but differs significantly in DNA and vocal patterns. Monotypic.

Distribution. SE Gabon, C Congo, S Zaire, S Uganda and SW Kenya, S to S Namibia, N Cape Province and Natal.



Descriptive notes. c. 22-24 cm; male 185-220 g, female 125-275 g. Differs from *P. leucotis* in darker and greyer coloration, bolder black markings with more contrasting white face, orange-red to red eyes, stronger talons. Juvenile with shorter ear-tufts, more obscure markings, yellow eyes. **Voice.** Bubbling "popopopo-popeeu", first part in fast stutter, second more fluting and rising in pitch.

Habitat. Savanna with scattered trees, thornveld, dry open woodland, woodland along rivers, and forest edge and clearings.

Food and Feeding. Large insects, spiders, scorpions; also small vertebrates, including

mammals, birds and reptiles; recorded taking some relatively large prey, up to size of bush squirrel (*Paraxerus*) and dove (*Streptopelia*). Foraging behaviour as for *P. leucotis*; large prey held in talons and torn apart with bill.

Breeding. Lays mainly May-Nov, with local dry-season peak in Jul-Aug. Nest in hole in tree trunk or branch, or in old stick nest of larger bird; at Zimbabwe one territory occupied 12 years; not specified if it was the same pair. 2-3 eggs; incubation from first egg, by female, period c. 30 days; chick with white down; young begin to leave nest at c. 27-28 days, can fly well at 30-32 days, cared for by parents for at least 2 more weeks. In Zimbabwe, 14 young fledged at 1 site over 6 years.

Movements. Generally resident. In drier parts of range fairly nomadic, making movements resulting in local irruptions; arrives after rains or when food abundant, may stay for only a few weeks and disappear again; attracted to grass fires, sometimes flying fairly long distances to capitalize on flushed insects and rodents.

Status and Conservation. Not globally threatened. CITES II. Reasonably common in most of range; scarce in Kenya, rare in N Tanzania, and probably rare generally at N limits of distribution. Occurs in a number of protected areas throughout its range, such as Lilongwe Nature Sanctuary in Malawi, Hwange (Wankie), Victoria Falls, Gona-re-Zhou and Rhodes Matopos National Parks in Zimbabwe, Moremi National Park in Botswana, Etosha National Park in Namibia, Gorongosa Reserve in Mozambique, and Kalahari Gemsbok and Kruger National Parks in South Africa.

Bibliography. Benson & Benson (1977), Benson *et al.* (1971), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Fry *et al.* (1988), Ginn *et al.* (1989), Harrison *et al.* (1997), Herholdt (1992), Kemp & Calburn (1987), Kemp & Kemp (1998), Lewis & Pomeroy (1989), Maas (1983), Mackworth-Praed & Grant (1957, 1962, 1970), Maclean (1993), Marshall, I. (1997), Mendelsohn (1989), Nuttall (1993), Penry (1994), Pickford *et al.* (1989), Pinto (1983), Priest (1939), Short *et al.* (1990), Snow (1978), Steyn (1982, 1984, 1994b), Worden & Hall (1978), Zimmerman, D.A. *et al.* (1996).

Genus *MIMIZUKU* Hachisuka, 1934

68. Giant Scops-owl

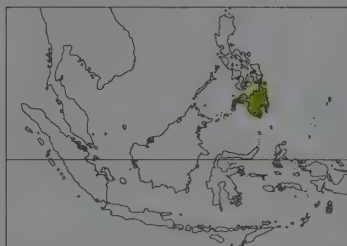
Mimizuku gurneyi

French: Petit-duc de Gurney **German:** Rotohreule **Spanish:** Búho de Mindanao
Other common names: Lesser/Mindanao Eagle-owl

Taxonomy. *Pseudopteryx gurneyi* Tweeddale, 1879, Zamboanga, Mindanao.

Formerly placed in an expanded *Otus*, but much larger than any of that genus, and distinct morphologically. Nevertheless, DNA studies indicate that it is closer to *Otus* than to *Bubo*; placement in a monotypic genus more appropriate pending further research. Monotypic.

Distribution. S Philippines: Dinagat, Siargao and Mindanao; report of former presence on Marinduque not confirmed.



Descriptive notes. 30 cm. Medium-sized owl, with long, well-developed, rufous ear-tufts marked with white; facial disc pale rufous, thinly outlined in black, with broad white eye-brows; dark rufous above with broad black shaft streaks, scapulars edged buffish-white; underparts white, washed rufous-buff on breast, and boldly streaked or spotted with dark brown; tarsi feathered white to toes; iris warm brown; bill yellowish to greyish; toes light grey. Juvenile undescribed. **Voice.** Has been recorded several times in recent years, but not description yet published.

Habitat. Lowland humid forest and secondary growth, from sea-level to c. 1200 m; recently reported from higher elevations, up to 3000 m.

Food and Feeding. No information.

Breeding. On Mt Katanglad, Mindanao, birds were vocally active in Feb. No other information.

Movements. Resident.

Status and Conservation. **ENDANGERED.** CITES I. Restricted-range species: present in Mindanao and the Eastern Visayas EBA. Appears to be rare in most of range, and thought to be a species that occurs at naturally low densities. Rapidly declining as a result of habitat destruction. May not be so rare as believed: on Mindanao, at 900-1200 m, call playback elicited responses from several individuals; postulated that, although many sympatric species are seriously threatened by forest clearance, most montane species may not yet be in extreme danger. Recent sightings from Mt Apo and Mt Katanglad, at higher altitudes, where adequate habitat still remains. Possibility that it occurs on other islands nearby where suitable habitat exists requires investigation.

Bibliography. Anon. (1997b), Clark & Mikkola (1989), Collar *et al.* (1994), Delacour & Mayr (1945, 1946), Dickinson *et al.* (1991), Hachisuka (1934), Marshall (1978), McGregor (1909-1910), Miranda *et al.* (1997), Oliver & Wirth (1996), duPont (1971, 1972), duPont & Rabor (1973b), Stattersfield *et al.* (1998).



ssp virginianus

69

ssp subarcticus

70

ssp bubo

71

ssp kiautschensis

ssp saturatus

ssp pallescens

72

ssp sibiricus

ssp ascalaphus

73

ssp desertorum

ssp capensis

74

ssp mackinderi

grey morph

75

76

77

78

inches 10
cm 25

PLATE 10

Tribe BUBONINI

Genus *BUBO* Duméril, 1806

69. Great Horned Owl

Bubo virginianus

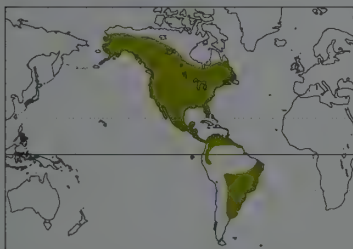
French: Grand-duc d'Amérique German: Virginiauhu Spanish: Búho Americano

Taxonomy. *Strix virginiana* J. F. Gmelin, 1788, Virginia.

Has sometimes been considered to belong to the *B. bubo* superspecies. Formerly included *B. magellanicus* as a race, but DNA, voice and morphology found to differ. Numerous geographical races named, many poorly differentiated, or apparently result of individual variation, or due to wandering birds from other parts of range: thus, forms described from coastal W Alaska (*algestus*), C Canada (*scalariventris*), Venezuela (*scotinus*), E Colombia (*elutus*), C Colombia (*colombianus*) and E Brazil (*deserti*) considered not acceptable; also, name *occidentalis* used for birds from Rocky Mts of WC Canada to WC USA, but now synonymized with *subarcticus*; older name *wapacuthu* formerly applied to populations of W & C Canada and N USA (limits uncertain), but validity questioned; in addition, N populations *lagophonus* and *heterocnemis* possibly not separable from *saturatus*, perhaps better merged with latter; boundaries of races often obscure, and problem further complicated by birds of intermediate appearance; races *pacificus* and *pallidus* intergrade in California. Pending further study, twelve races tentatively recognized.

Subspecies and Distribution.

B. v. lagophonus (Oberholser, 1904) - Alaska, S in mountains to NE Oregon and NW Montana; in winter S to Texas.
B. v. saturatus Ridgway, 1877 - coast from SE Alaska to N California.
B. v. pacificus Cassin, 1854 - coast of California (except N) S to NW Baja California.
B. v. elachistus Brewster, 1902 - S Baja California.
B. v. subarcticus Hoy, 1853 - Mackenzie and NW British Columbia E to Hudson Bay, S at least to Wyoming and North Dakota; possibly this race, or intermediates between it and *pallidus* and/or *lagophonus*, or unnamed race, S to Arizona, New Mexico and SW Texas (Guadalupe Mts).
B. v. pallidus Stone, 1897 - C California (San Joaquin Valley) and deserts of SE California E to W Kansas, S to Mexico (S to Guerrero, W Veracruz).
B. v. heterocnemis (Oberholser, 1904) - NE Canada S to Great Lakes region.
B. v. virginianus (J. F. Gmelin, 1788) - Minnesota E to Nova Scotia and Prince Edward I, S through E Kansas and E Texas to Florida.
B. v. mayensis Nelson, 1901 - Yucatán Peninsula.
B. v. mesembrinus (Oberholser, 1904) - from Isthmus of Tehuantepec to W Panama.
B. v. nigrescens Berlepsch, 1884 - Andes from Colombia to NW Peru.
B. v. nacurutu (Vieillot, 1817) - lowlands from E Colombia to the Guianas; also Bolivia across to NE Brazil, S to EC Argentina (Buenos Aires).



Descriptive notes. Male 51 cm, wingspan 134 cm, 680-1450 g; female 60 cm, wingspan 143 cm, 1000-2500 g. Large, powerful owl, ear-tufts large and erect, plumage distinctly greyish to grey-brown or more buffy-brown, mottled and vermiculated above, barred below, with white throat; wings long and broad, pointed towards tip. Nominally *virginianus* with facial disc dull tawny-buff to distinct orange-buff, whitening around eyes, black rim broken by grey-buff flecking at lower edge; crown and hindneck dark; upperparts brownish with rufous tinge, mottled dark sooty-brown, broken by transverse mottlings of tawny grey-white.

wing-coverts and scapulars mottled with buff- to grey-white; flight-feathers and tail distinctly and regularly barred dark slate-grey to brown-black; underparts usually slightly sooty grey-buff with bold and somewhat erratic barring of brown-black, bars more pronounced on flanks and lower belly, and broad area of pure white on throat narrowing to upper breast; tarsus and feet fully feathered tawny to buff, often with black barring; iris brilliant yellow; bill grey; talons brownish yellow-horn, darkening to black at tip. Juvenile somewhat more ruddy brown-orange, bars farther apart, white throat patch duller and much less extensive, ear-tufts shorter. Races vary in size, tending to become smaller from NE to SW, small in S of range, and tend to be darker in more humid regions: *lagophonus* rich tawny-grey, feet barred; *saturatus* dark brownish-grey, heavily barred below; *pacificus* fairly dark, suffused tawny, less heavily barred, *elachistus* similar but much smaller; *subarcticus* pale whitish-buff, variably barred below, feet more or less plain; *pallidus* small, pale, barring above and below relatively indistinct, feet whitish; *heterocnemis* dark grey-brown, heavily barred below, feet mottled; *mayensis* small, short-winged, rather pale, *mesembrinus* similar but larger and darker; *nigrescens* dark, heavily blotched; *nacurutu* browner, longer-billed. **VOICE.** Male during courtship utters "hu-huooooo, hooh hooh" of c. 3 seconds; female higher-pitched with extra note at beginning, "hu-huuhoo hooh hooh"; also loud screams.

Habitat. Wide range of wooded habitats, mainly open, from deciduous to mixed and coniferous forest, second growth, swamp-forest, farmland with patches of woodland, larger parks in towns, and mangroves; generally with open fields adjacent or nearby; also roadsides; locally, desert and rocky areas with some woodland. Foraging areas typically relatively open, but also include some woodland or groves, or at least scattered trees for perching. Sea-level to c. 4000 m; in Andes to 4500 m.

Food and Feeding. Very diverse range of prey includes small mammals, birds, amphibians, reptiles, fish, and insects and other invertebrates; sometimes takes carrion when weather conditions severe. Mammals generally most important, often c. 90% of diet; lagomorphs, mice and waterbirds major food in many areas. Birds average c. 10% of food, range in size from small passerines up to geese and Great Blue Heron (*Ardea herodias*), and include other raptors; also nestlings. In N Canada, snowshoe hares (*Lepus*) represent 83-86% to 13% of diet, depending on hare density; alternative

prey mainly voles (*Microtus*), ground squirrels (*Spermophilus*) and birds. In Argentina, mammals also majority of prey (69%); arthropods an alternative, with beetles (21%) and scorpionids (5%) most common, and birds, reptiles and amphibians poorly represented. Forages mostly at dusk and during night, rarely in daylight, usually in fairly open areas offering wide view, e.g. forest edge or clearings, or along wetland margins, also over open water. Hunts from perch, dropping steeply to ground and levelling off just above it; also flaps and glides over places where prey likely to be; occasionally forages by walking on ground, and reported to wade into water. Prey seized in talons; smaller items swallowed whole, larger ones dismembered first.

Breeding. Season approximately Dec-Jul; female observed to incubate in sub-zero temperatures, with 30-cm snow cover on ground. Normally uses old nest of other large bird such as corvid or raptor, in N often Red-tailed Hawk (*Buteo jamaicensis*), high up in main fork of tree, sometimes in heronry; also hollow at broken-off snag, or man-made platform, or depression on cliff ledge or ground, or cave entrance (in Ohio study, 533 in hawk nest, 527 in snag, 125 on man-made platform); rarely on building, once on beam beneath railway bridge; no material added; may use same nest 2-3 years in succession. In courtship display, both sexes hoot while bowing and while simultaneously drooping wings and cocking tail. 1-3 eggs, usually 2, up to 6 in food-rich years, laying interval averaging 72 hours; clutch often replaced if first destroyed; incubation c. 28-30 days, sometimes up to 37, by female, fed regularly through night by male; rarely, latter recorded incubating briefly; chick with white down, pink apteria and feet; young brooded by female until c. 2 weeks, climb on nearby branches at 6-7 weeks, fly well from c. 10 weeks; subsequent parental care up to 5 months. In USA (Ohio), mean annual productivity 1.7 young per successful nest, 1.3 young per breeding attempt, 15% of breeding pairs failed, 38% of pairs did not attempt to nest, average 0.80 young per occupied territory; in one study, mortality highest during post-fledging period, with 13 deaths due to high levels of parasitism, 11 to predation (or with signs of scavenging), 9 to disease, starvation or cause unknown, 6 roadkills; survival in first 2 years of life low, but higher during peaks in hare cycle. First breeding probably at 2 years, sometimes 1. Maximum recorded longevity more than 28 years.

Movements. Mostly resident, but some movement by N birds. In Canada (Saskatchewan), substantial SE movement in Nov-Dec in some years, with 17 of 35 recoveries occurring beyond 250 km from point of ringing; evidently, moves farther S during years of decreased reproductive success and, presumably, reduced food supplies.

Status and Conservation. Not globally threatened. CITES II. Widespread, but densities low; few population estimates. Commonest owl in S Quebec; in optimum habitat in North America, densities of 0.1-0.2 pairs/km², in S of range rather scarce generally, but said to be quite common in S Mato Grosso in Brazil. Population levels closely associated with prey availability: when prey scarce, breeding density much lower and mortality sometimes very high; in periods of high prey abundance, higher survival leads to greater intraspecific (and interspecific) competition. Heavily persecuted in first half of 20th century, but totally protected in North America since 1970; probably reasonably stable now within limits of annual fluctuations. In Canada, however, presence of individuals referred to as "non-territorial floaters" (a "shadow" population that lives a secretive life, moves more often than territorial birds, and ranges broadly over territories of latter) can delay detection of population declines in traditional censuses. Roadkills, pesticides, collisions with man-made objects, electrocution from power lines, and indiscriminate and illegal shooting are major causes of mortality locally in USA (Utah); these factors likely to be applicable elsewhere in range. Habitat disruption apparently less of a threat, and range and numbers noted to have expanded in Pacific Northwest following opening-up of new areas by logging activities. Species' continuing survival almost throughout range aided perhaps by its highly secretive nature and its high capacity for ecological adaptability; adapts well to changes in habitat, so long as suitable nest-sites and roost-sites remain.

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70. Magellanic Horned Owl

Bubo magellanicus

French: Grand-duc de Magellanie German: Magellanuhu Spanish: Búho Magallánico
Other common names: Magellan Great Horned Owl, Lesser Horned Owl

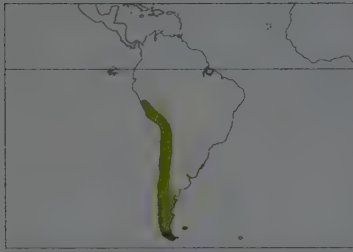
Taxonomy. (*Strix*) *magellanicus*, J. F. Gmelin, 1788, Straits of Magellan.

Until recently included as a race of *B. virginianus*, but differs in vocalizations and morphology, and also in DNA; in past, occasionally even merged with *B. v. nacurutu*. Monotypic.

Distribution. From C Peru, W Bolivia and W Argentina, S to Tierra del Fuego and Cape Horn.

Descriptive notes. c. 45 cm. Very like *B. virginianus*; differs in smaller size, smaller ear-tufts, smaller bill, weaker talons, more prominent rim around facial disc, narrower and more closely spaced barring below; general coloration varies from grey-brown to darker brown. Juvenile much as *B. virginianus*. **VOICE.** Male song 2 deep hoots, second one stressed, followed by low quiet purring sound, "huOOH-urrrr"; female gives longer purr; duets in courtship.

Habitat. Rocky upland pasture, semi-open forest (especially *Nothofagus*), Patagonian steppe and semi-desert with scattered trees, bushy ravines and surrounding grassland; in S, also parks in areas of human settlement. In Andes mostly at 2500-4500 m; locally down to sea-level.



Breeding. Season begins late winter. Nest in crevice or rock overhang; sometimes depression on ground in forest. 2-3 eggs; incubation by female, fed by male; young leave nest before able to fly, remain nearby.

Movements. Resident; some birds in extreme S move N in winter; juveniles sometimes wander longer distances.

Status and Conservation. Not globally threatened, CITES II. Seems to be common in Chile and Patagonia. Numbers in C Chile increased after introduction of rabbit (*Oryctolagus cuniculus*) in 1907. Main threat appears to be human persecution, which locally quite severe; poisoned baits for foxes in Patagonia may be a potential threat, although no known deaths from such causes reported; road casualties also quite frequent.

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71. Eurasian Eagle-owl

Bubo bubo

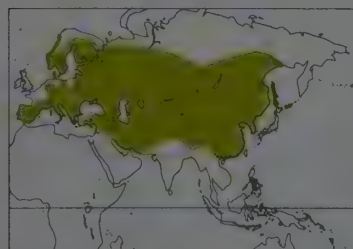
French: Grand-duc d'Europe **German:** Uhu **Spanish:** Búho Real
Other common names: Common/Great/Northern Eagle-owl

Taxonomy. *Strix Bubo* Linnaeus, 1758, Sweden.

Forms superspecies with *B. bengalensis* and *B. ascalaphus*, with *B. virginianus* (including recently separated *B. magellanicus*) and *B. capensis* sometimes considered part of same group. Sometimes considered to include first two as races; appears to intergrade with *B. ascalaphus* in parts of Middle East, suggesting that conspecificity perhaps not impossible. Geographical boundaries of races obscured throughout by intergrading populations. Large number of additional races named, some representing no more than individual variation or intermediates; e.g. populations described from Bashkirskaya (*bashkiricus*) included in *sibiricus*; from L Zaysan region (*zaisanensis*) in *yeniseensis*; from NW Xinjiang (*tarimensis*) in *turcomanus*; from C Tibet and NW China (*tibetanus*) in *hemachalana*; from N Mongolia (*dauricus*) and Sakhalin (*borissowi*) in *ussuriensis*; from SE Yunnan (*jarlandi*), Sichuan (*seichuanus*), Manchuria and N China (*inexpectatus*) in *kiautschensis*; and from S Kurils, Hokkaido and Korea (*tenuipes*) split between *ussuriensis* and *kiautschensis*. Fourteen subspecies recognized.

Subspecies and Distribution.

- B. b. hispanus* Rothschild & Hartert, 1910 - Iberian Peninsula; formerly also Atlas Mts in NW Africa (probably extinct).
- B. b. bubo* (Linnaeus, 1758) - Europe from N Spain and Scandinavia E to W Russia (E to about Gor'kiy).
- B. b. ruthenus* Buturlin & Zhitkov, 1906 - C European Russia E to foothills of Ural Mts, S to lower Volga basin.
- B. b. interpositus* Rothschild & Hartert, 1910 - from Romania and S Ukraine E to Volga delta, S to Middle East (S to C Israel and Jordan) and NW Iran.
- B. b. sibiricus* (Gloger, 1833) - from W foothills of Urals E to R Ob, S to W Altai.
- B. b. yeniseensis* Buturlin, 1911 - C Siberia from R Ob to L Baikal, S to Altai and N Mongolia.
- B. b. turcomanus* (Eversmann, 1835) - steppes between lower R Volga and R Ural, E to Transbaikalia, and S to Kazakhstan, extreme NW China (Tarim Basin in NW Xinjiang) and W Mongolia.
- B. b. omissus* Dementiev, 1932 - Turkmeniya to W China (Chinese Turkestan).
- B. b. hemachalana* Hume, 1873 - from Pamirs and N Tien Shan S to Himalayas.
- B. b. nikolskii* Zarudny, 1905 - E Iraq and Iran, Afghanistan, and N & W Pakistan.
- B. b. jakutensis* Buturlin, 1908 - NE Siberia.
- B. b. ussuriensis* Poljakov, 1915 - SE Siberia to NE China, Sakhalin, N Hokkaido and S Kuril Is.
- B. b. kiautschensis* Reichenow, 1903 - from W & C China (S to Yunnan and Sichuan) E to Korea.
- B. b. swinhoei* Hartert, 1913 - SE China.



on flanks and belly; tarsus and toes fully feathered buff-white; iris golden to orange; bill black. Juvenile with rudimentary ear-tufts, head with buffy down, underparts and wing- and tail-coverts narrowly barred. Races differ mainly in general coloration, strength of dark markings, and size: *hispanus* and *ruthenus* lighter and greyer than nominate; *interpositus* darker, more rufous; *sibiricus* very pale, creamy-white below with contrasting streaks; *yeniseensis* darker, with yellow ground colour; *hemachalana* more light brown above, including mantle, *turcomanus* similar but greyer; *omissus* with ochre ground colour, markings below less heavy, *nikolskii* smaller and more rufous; *jakutensis* dark, browner above, well marked below, *ussuriensis* darker still with ochre wash below; *kiautschensis* rather small, very dark, streaking thin; *swinhoei* small, strongly tinged rufous. Voice. Territorial call a booming "boo-ho" or "ooo-hu", first syllable emphasised, second lower,

Food and Feeding. Mostly small mammals up to size of rabbits and hares; also birds, reptiles and some invertebrates. A pellet analysis in C Chile revealed 69.3% rodents, 15.8% rabbits and 11.4% birds; in a study in S Chile, diet consisted solely of rodents, with *Auliscomys micropus* and *Abrothrix longipillus* together forming 60.4% of prey in terms of numbers captured and 74.4% of biomass consumed. Hunts mostly at dusk and dawn, sometimes nocturnally; also by day in S of range, where close to 24-hour daylight during summer. Foraging methods similar to those of *B. virginianus*; often uses rock as lookout perch.

repeated every 8-10 seconds; female higher-pitched, hoarser; duets in courtship; female also barking scream; alarm harsh "ka ka-kau".

Habitat. Tends to inhabit regions of sparse human settlement or areas of topographically inaccessible terrain: mainly rocky country with cliffs and ravines, caves, patches of woodland, scattered trees or groves, generally in undisturbed wilderness areas; also open forest, taiga and other types of woodland, wooded steppe, river valleys with gorges, overgrown quarries; also farmland with suitable rocky areas or cliffs. Forages also over open or sparsely wooded terrain, as well as floodland, heaths, farmed valley bottoms or levels with grassland, small arable fields, and even refuse dumps. Breeds from sea-level up to c. 2000 m in Europe; 4200-4500 m in C Asia and Himalayas.

Food and Feeding. Mostly mammals, from size of water vole (*Arvicola*) to adult hares (*Lepus*), and birds from size of jay (*Garrulus*) to herons (Ardeidae) and buzzard (*Buteo*); also occasionally amphibians, reptiles, fish, and invertebrates (especially beetles). Preferred prey size in range 200-2000 g. In C Europe lagomorphs important prey, also hedgehogs (*Erinaceus*) locally; in China, mainly rats and mice. Diet can vary according to prey abundance and season; in Sweden, rodents taken in proportion to their population levels, ranging from 23% to 65% in different years, and adult hares increase in importance in late winter, with other prey (e.g. fledgling birds) becoming important when available; in Finland, 1 pair's diet largely water voles when abundant, switched to brown rats (*Rattus norvegicus*) from nearby rubbish dump at other times; in Spain, proportion of birds in diet may increase in spring and summer, and shortage of rodents compensated for by increase in birds. Cannibalism occurs, with weakest young eaten by parents or siblings, and occasionally a full-grown bird recorded eaten by conspecifics. Primarily nocturnal, somewhat crepuscular, even diurnal in summer at N edge of range. Hunts mostly from open perch; also in searching flight; takes prey by surprise while flying close to ground or tree-tops; sometimes makes systematic searches of rock crevices for roosting birds; usually watches and waits for prey to reveal itself, but also recorded jumping around looking for Common Eiders (*Somateria*) on nest. Said also to take birds in full flight, to seize fish by plunging into water like Osprey (*Pandion haliaetus*), and to plunder both adults and young of nest of e.g. crows (*Corvus*) over 1-2 nights.

Breeding. Season Feb-Aug in Scandinavia; laying from Dec in France. Monogamous; solitary. Nest on sheltered cliff ledge or in crevice, in cave entrance, on ground on steep slope or on flatter ground in taiga, sometimes in old tree nest of other species, rarely in hole in tree; same site often used over several years, or favoured sites in territory used partly in rotation. 2-4 eggs, occasionally 1, laying interval 3 days; incubation 34-36 days, by female, fed by male; hatching asynchronous, chick with whitish and buffy down; young brooded by female, continuously for c. 15 days, male feeds female and young; after 3 weeks young start to feed themselves at nest, move outside nest at 5 weeks (earlier in case of ground nests), can fly at c. 7 weeks; young independent at 20-24 weeks. In Sweden, of 219 occupied territories, 66% had active nests, of which 60% produced fledged young, making total of 136 young produced, and averages of 1.6 young per successful nest, 0.9 per active nest and 0.6 per occupied territory; production varied according to food supply; losses attributed to starvation, predation, and human disturbance, including egg-collectors; extremely sensitive to disturbance, parents may abandon eggs and even small young. First breeding at 2-3 years. Oldest known age at least 21 years; up to 60 years reported in captivity.

Movements. Resident in most of range; juveniles disperse variable distances, recorded as vagrant in Nile valley. In N of range, some move S in winter, depending on food availability; in harsh winter conditions of N & C Asia, can be highly nomadic.

Status and Conservation. Not globally threatened, CITES II. Uncommon to scarce or rare throughout range. Total European population (including W Russia and Turkey) in mid 1990's estimated at c. 25,000 pairs, of which c. 50% in Russia. Densities low in most areas, with maximum 1 pair/100 km² in C Europe; higher in S France, where 43-50 pairs in study area of 200 km²; c. 6 pairs/100 km² in Spain, and in Finland 2-13 pairs/100 km². Considerable decline in Europe in 20th century, with extinctions in e.g. Luxembourg and Denmark, and reductions in range and population elsewhere; in Sweden, widespread until late 19th century but extinct in many areas by c. 1920. In general, decreases due mainly to human persecution; significant decline in Mediterranean countries in 1960's apparently due to effects of myxomatosis on rabbit population; in addition, poisoning from mercury seed-dressings, and deaths through road traffic and barbed wire not insignificant. Fairly rapid post-1970 recovery in parts of Europe aided by protection and by extensive reintroduction programmes, especially in Germany, France, Belgium, Switzerland and Scandinavia, although reintroduced birds suffer high mortality and poor breeding success; increased food supply created by proliferation of refuse tips (rats) or large clearfelled areas (various rodents and birds) probably also a factor in promoting recovery. Nevertheless, overall trend almost certainly one of decline. No detailed data on Asian populations, but uncommon or rare everywhere, and marked decline noted in many areas since 1970's. Despite protected status, species still persecuted locally; pesticides and other toxic chemicals also remain a problem in some areas. Protection of nesting territories, and potential territories, from development and from extensive logging recommended.

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72. Rock Eagle-owl

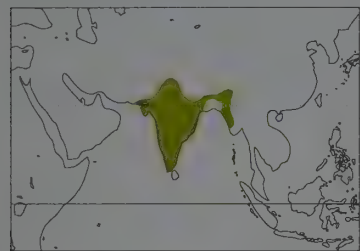
Bubo bengalensis

French: Grand-duc indien **German:** Bengalenuhu **Spanish:** Búho Bengali
Other common names: Indian Eagle-owl/Great Horned Owl

Taxonomy. *Otus Bengalensis* Franklin, 1831, River Ganges between Calcutta and Varanasi and in Vindhyan Hills between Varanasi and Gurra Mundela.

Forms superspecies with *B. bubo* and *B. ascalaphus*, with *B. virginianus* (including recently separated *B. magellanicus*) and *B. capensis* sometimes considered part of same group. Sometimes treated as conspecific with *B. bubo*; degree of range overlap, if any, with latter uncertain, but they differ in DNA and voice. Monotypic.

Distribution. Indian Subcontinent (except Sri Lanka), N to foothills of Himalayas, and W Myanmar.



Descriptive notes. 56 cm; 1 male c. 1100 g. Large, dark brown owl with prominent ear-tufts. Resembles *B. bubo*; differs from race *hemachalana* of latter in smaller size, darker and more tawny-buff coloration with black mottling and streaking, somewhat less heavy streaking below; iris golden to orange-yellow or reddish; bill horn, greenish or slaty-black. Dark and light morphs, former having darker ground colour with fewer light spots above. Distinguished from *Ketupa zeylonensis* by fully feathered tarsi and toes, more erect ear-tufts, broader breast streaking, and plainly banded tail. Juvenile lacks ear-tufts, obscurely barred

on head, mantle and underparts. VOICE. Deep double hoot, with second note longer and stressed; female a little higher-pitched; also growls, hisses, coughs.

Habitat. Rocky hills and wooded country with scrub, ravines, old mango plantations, groves with aged trees, tropical thorn and sal, and rocky semi-desert with thorn scrub, ruins; sometimes near cultivation and villages; avoids pure desert, as well as humid evergreen forest. From lowlands up to 2400 m.

Food and Feeding. Small mammals, especially rodents; also birds to size of peafowl (*Pavo*), and lizards, snakes, frogs, fish and crabs; some insects, too. Largely nocturnal, but often perches on rock pinnacle or other vantage point well before sunset and after sunrise. Hunts by gliding from perch on to prey; sometimes makes searching flights.

Breeding. Lays Oct-May, chiefly Feb-Apr; peak periods vary locally. No nest; lays on bare soil in saucer-like scrape on rock ledge or recess in cliff; sometimes on ground under tree or bush. Usually 4 eggs (2-5); incubation from first egg, by female, period c. 35 days; young hatch asynchronously; chick with buffish-white down.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. No details on population levels; generally uncommon, but perhaps more common locally in N and C India. Further studies needed on ecology and biology.

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73. Pharaoh Eagle-owl

Bubo ascalaphus

French: Grand-duc du désert

German: Wüstenuhu

Spanish: Búho Desértico

Other common names: Desert/Savigny's Eagle-owl

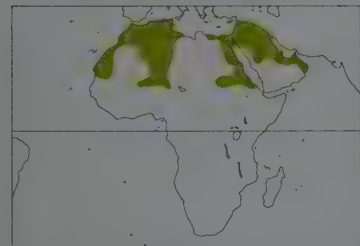
Taxonomy. *Bubo Ascalaphus* Savigny, 1809, Upper Egypt.

Forms superspecies with *B. bubo* and *B. bengalensis*, with *B. virginianus* (including recently separated *B. magellanicus*) and *B. capensis* sometimes considered part of same group. Formerly treated as conspecific with *B. bubo*; separation based mainly on vocalizations, and partly morphology, but DNA evidence not conclusive; also, appears to intergrade with *B. bubo* in parts of Middle East, suggesting that conspecificity perhaps possible; on other hand, some range overlap without known intermediates with *B. bubo* race *hispanus* in NW Africa, although latter now presumed extinct there; further study warranted. Two subspecies recognized.

Subspecies and Distribution.

B. a. ascalaphus Savigny, 1809 - NW Africa and N Egypt E to W Iraq.

B. a. desertorum Erlanger, 1897 - Sahara S to Mauritania and Niger, E to Ethiopia, Arabia and S Iraq.



Descriptive notes. 46-50 cm; male c. 1900 g, female c. 2300 g. Facial disc light tawny-rufous with darker rim; tawny head and neck streaked with dark brown; upperparts tawny with black streaks and blotches, buffish mottling; flight-feathers less distinctly barred; conspicuous white throat patch; sandy-rufous below, chest with broad black streaks, lower breast to belly with very fine vermiculations; underwing almost white; tarsus fully feathered; iris yellow to orange; bill black. Distinguished from *B. bubo* by smaller size (c. 20% smaller), shorter ear-tufts, paler appearance, less streaked and more mottled; from *B. capensis* by paler

and less variegated plumage. Juvenile more barred than blotched on upperparts and breast, ear-tufts not fully developed. Race *desertorum* slightly smaller and paler, more sandy, with very pale underparts. VOICE. Single deep, downslurred "whu"; in courtship also 3-note hoot; voice slightly higher than *B. bubo*; quacking call in alarm.

Habitat. Rocky desert hills, wadis with cliffs, and open desert with rock outcrops; extends S into dry savanna in S. Roosts by day in rock cleft or crevice, occasionally in tree if present.

Food and Feeding. Small mammals, especially rodents, with gerbils (*Gerbillus*) favoured prey; also birds and reptiles, and some insects. Generally opportunist, taking any animal food available, including desert foxes, hares, bats and scorpions. Crepuscular or nocturnal; hunts from perch.

Breeding. Lays Feb-Mar. Monogamous; pairs for life. Nest a scrape in rock crevice, among rocks or on ground, sometimes down well (in darkness); sometimes old nest of large bird or tree hole in desertified areas of sub-Sahara: same territory maintained for many years. Usually 2 eggs, but up to 4; incubation by female, fed by male, period 31-36 days; chick with buffish-white down; young brooded and fed by female, male provides food; disperse from nest at 20-35 days, fully fledged at 52-70 days, independent by 20-26 weeks. First breeding at 2-3 years.

Movements. Resident; presumably some wandering by juveniles.

Status and Conservation. Not globally threatened. CITES II. Little information on population levels, but probably not uncommon in most of range. In S Israel, c. 50 pairs estimated in early 1990's. Possibly subject to human persecution locally.

Bibliography. Amr *et al.* (1997), Aspinall (1996), Bannerman (1953), Beaman (1994), Beaman & Madge (1998), Boukhamza *et al.* (1994), Carpentier (1934), Cave & Macdonald (1955), Cramp (1985), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Échécopar & Hùe (1964), Evans (1994), Evans & Bates (1993), Fry *et al.* (1988), Giraudoux *et al.* (1988), Goodman *et al.* (1989), Hùe & Échécopar (1970), Jennings (1995), Kemp & Kemp (1998), Ledant *et al.* (1981), Lesne & Thevenot (1981), Mackworth-Præd & Grant (1957, 1970), Mendelsohn (1996), Paz (1987), Porter, Christensen & Schiermacker-Hansen (1996), Sellami & Belkacemi (1989), Sharland, R.E. (1981), Shirihai (1996), Snow (1978), Snow & Perrins (1998), Vein & Thevenot (1978), Voous (1988).

74. Cape Eagle-owl

Bubo capensis

French: Grand-duc du Cap

German: Kapuhu

Spanish: Búho de El Cabo

Other common names: Dillon's/Mountain Eagle-owl (*dillonii*); Mackinder's Eagle-owl (*mackinderi*)

Taxonomy. *Bubo Capensis* A. Smith, 1834, near Cape Town, South Africa.

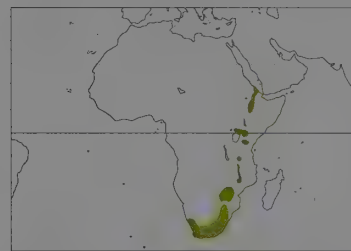
Affinities uncertain. Formerly thought to be member of *B. bubo* superspecies, but seems more distantly related. Race *mackinderi* has been considered a full species, but differences minor. Three subspecies recognized.

Subspecies and Distribution.

B. c. dillonii Des Murs & Prévost, 1846 - S Eritrea and Ethiopian Highlands.

B. c. mackinderi Sharpe, 1899 - from WC Kenya S to Zimbabwe and W Mozambique.

B. c. capensis A. Smith, 1834 - South Africa and extreme S Namibia.



Descriptive notes. 48-58 cm; wingspan c. 120 cm; male 900-1400 g, female 1200-1800 g. Large, with long, pointed ear-tufts. Generally dark brown. Facial disc pale buff-brown with blackish border; dark brown above with light tawny and buff spotting, wing-coverts variably spotted white; flight-feathers and tail barred; throat white; underparts creamy buff-brown, breast with heavy dark blotching, flanks spotted and abdomen barred; tarsus and toes thickly feathered; iris orange to orange-yellow; bill dark greyish. Differs from *B. africanus* in larger size, orange eyes, browner plumage and breast markings. Juvenile largely grey with rufous

barring, wings and tail as adult; indistinct ear-tufts. Races separated by size: *mackinderi* largest, darker above; *dillonii* almost as big, darkest. VOICE. Deep hoot, "hoooo-ho", first note loud and second weak, also 3-note "hu-hoo-hu"; female higher-pitched; occasional duets.

Habitat. Wooded valleys, low cliffs and ravines, in rocky mountainous terrain from 2000 m to 4200 m; hunts also over adjacent open rocky slopes and grassland. In S. occurs also in flat, dry and open country.

Food and Feeding. Mid-sized mammals, mainly hares and hyraxes, but including bats, rats and mole-rats; also birds, especially pigeons and gamebirds, but up to size of Hamerkop (*Scopus umbretta*); occasionally reptiles and amphibians, scorpions and insects. Crepuscular and nocturnal. Hunts by surveying area from prominent perch, and descending upon prey in long glide; also engages in aerial chases.

Breeding. Lays Jul-Mar in E Africa, Jul in S Africa; in SW Cape in Jun-Aug, in E Cape Aug-Sept; irregular breeder, attempting every 10-11 months or 2-3 years, possibly depending on prey abundance. Nest an unlined scrape on sheltered cliff ledge, or in cave entrance, or beneath bush on ground; occasionally uses old stick nest of large bird; thick, enamel-like droppings on ledge often clue to active nest; large accumulations of bones from prey form ossuaries near nest. 1-3 eggs, usually 2; incubation 34-36 days, by female, fed by male; chick with whitish down; young brooded and fed by female, male delivers prey during night; young begin to wander outside nest at 45 days, can fly by 60-77 days (smaller nominate *capensis* fledging earliest), dependent on parents for at least 2-3 months after fledging. In Kenya 60% of eggs laid fledged young, in Zimbabwe 50%; cannibalism of younger siblings regular.

Movements. Generally resident; young birds may wander widely, occasionally occurring in cities and outside normal range.

Status and Conservation. Not globally threatened. CITES II. Generally uncommon to rare, and very local; more common in some places, e.g. Mau Plateau in SW Kenya, but easily overlooked and never at high densities. Most widespread in S Africa at low altitudes; to N, range more fragmented and confined to mountains. Predation of ground nests, along with road-traffic casualties, collisions with power lines and entanglement on barbed-wire fences, seem to be main threats; young reportedly taken by humans for pets, often die or left crippled through improper feeding.

Bibliography. Allan (1995), Benson & Benson (1977), Brooke (1973b), Burger (1980), Clinning (1980), Daugherty (1981), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Fry *et al.* (1988), Gamble (1979), Gargett (1976, 1977a, 1977b, 1978, 1983), Gargett & Grobler (1976), Ginn *et al.* (1989), Grobler (1980, 1982), Harrison *et al.* (1997), Hockey *et al.* (1989), Jackson (1973b), Kemp & Calburn (1987), Kemp & Kemp (1998), Lewis (1978), Lewis & Pomeroy (1989), Mackworth-Præd & Grant (1957, 1962), Maclean (1993), Martin & Pepler (1977), Mathews & Scott (1980), Medland (1989), Pickford *et al.* (1989), Rossouw (1993), Rutledge (1986), Sessions (1972), Short *et al.* (1990), Snell (1979), Snow (1978), Steyn (1982, 1984, 1992, 1994c), Steyn & Tredgold (1977), Taylor (1987), Walter *et al.* (1986), Weiss & Weiss (1993a, 1993b), Zimmerman, D.A. *et al.* (1996).

75. Spotted Eagle-owl

Bubo africanus

French: Grand-duc africain

German: Fleckenuhu

Spanish: Búho Africano

Other common names: African Eagle-owl

Taxonomy. *Strix africana* Temminck, 1821, Cape of Good Hope, South Africa.

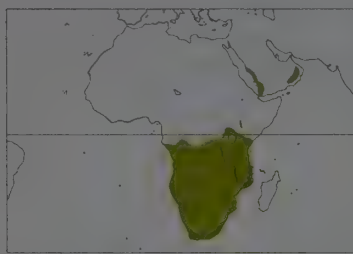
Often considered to include *B. cinerascens* as a race, but the two differ in morphology and not known to interbreed where ranges overlap. Taxonomic status of race *milesi* not well understood, possibly specifically distinct. Race *tanæae* perhaps only pale variant, as is form described from Namibia (*trothæ*). Three subspecies recognized.

Subspecies and Distribution.

B. a. milesi Sharpe, 1886 - SW Arabia, Yemen and Oman.

B. a. africanus (Temminck, 1821) - Gabon E to Zaire (S of rainforest), S Uganda and C Kenya, S to the Cape.

B. a. tanæae Keith & Twomey, 1968 - R Tana and Lali Hills, in SE Kenya.



Descriptive notes. c. 45 cm; wingspan c. 100 cm; male 490–620 g, female 640–850 g. Rather small eagle-owl with long, erect ear-tufts. Facial disc grey with faint white bars, outlined in black; head and neck brown-grey with white to buff spots, including ear-tufts; upperparts grey to brown with pale spots, flight-feathers and tail broadly banded in buff; whitish below, finely barred grey-brown, upper breast often with large grey blotches; tarsus feathered whitish, faintly barred; iris yellow; bill black. In more arid areas rarer chestnut-brown morph, with ground colour browner above and buff below, eyes orange. Differs from *B. capensis* in smaller size, yellow eyes, and greyer plumage. Juvenile waspish browner below, less spotted above. Race *milesi* smaller, more tawny; *tanai* paler, less barred. **VOICE.** Male gives "hoo-hoo", second note lower, followed by 3-note hoot plus longer note, also single notes or various combinations; female triple "hoo-whoohoo"; often duets, female following so closely that calls sound like one; loud "kiow" in alarm.

Habitat. Variety of habitats, from rocky outcrops in desert to woodland with sparse ground cover; particularly favours areas with mosaic of low hills, grassland and scrub; prefers semi-open woodland, and rocky hills with scattered trees and bushes; also found in thorn savanna; avoids dense forest. From sea-level up to c. 2100 m.

Food and Feeding. Opportunist, taking mainly arthropods, small mammals and birds. Large number of different types of prey recorded: arthropods include scorpions, spiders and beetles; mammals include moles, rodents, hedgehogs and bats; birds range from sunbirds and doves to falcons, hornbills and francolins; also reptiles, amphibians, snails, and freshwater crabs. Diet related to locality and season: in Namib Desert mainly geckos, gerbils and moles, but in South Africa 67% of 1076 prey items were invertebrates; along coast, a pair fed mostly on terns; rodents major prey when abundant. Occasionally eats carrion; regularly drinks water. Crepuscular and nocturnal, rarely diurnal. Hunts from perch, often along roadsides, gliding down on to prey; most prey taken on ground, where often runs after smaller animals; also chases insects, bats and birds aerially.

Breeding. Lays in Jul–Feb; mainly Jul–Oct in S Africa. Monogamous, probably pairs for life. Nest a shallow scrape, usually on ground beneath bush, among grass or rocks or on earth bank, but can be on cliff ledge, or on old platform built by Hamerkop (*Scopus umbretta*), or using Social Weaver (*Philetairus socius*) colony as platform; sometimes in hole in tree or building; same site sometimes used yearly, giving it distinctive odour; traditional sites may be occupied for 30–40 years. 2–4 (1–5) eggs; incubation 30–32 days, from first or second egg, by female, fed by male; chick with white down; young brooded and fed by female, male delivers prey usually decapitated; young leave nest at 30–38 days, later if nest above ground, fledge at c. 48 days, dependent on parents for at least 5 weeks after fledging, but exact age of independence unknown. Success generally high: at a site in Rwanda, young reared in 14 of 15 seasons; in Zimbabwe, 11 young fledged from 12 eggs; sometimes double-brooded if food abundant. First breeding possibly at 1 year old. Longevity of at least 10 years recorded.

Movements. Generally resident; local vertical movements recorded in Malawi, moving to higher elevations during hot summers.

Status and Conservation. Not globally threatened. CITES II. Widespread throughout S half of Africa, where often the commonest strigid in many habitats. Few data on densities; in Zimbabwe, c. 3 pairs found in 6 km². Fairly common in Tanzania, uncommon in Uganda and Kenya. Sometimes hit by road vehicles, or becomes trapped in barbed-wire fences or thorn bushes; other threats include local human persecution.

Bibliography. Baron (1984), Benson & Benson (1977), Benson *et al.* (1971), Cooper & Cooper (1992), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Evans (1994), Friedmann (1930), Fry *et al.* (1988), Frylink & Frylink (1996), Ginn *et al.* (1989), Grobler (1980), Harrison *et al.* (1997), Herholdt (1986b), Hockey *et al.* (1989), Jennings (1995), von Kaschke (1992), Kemp, A.C. & Calburn (1987), Kemp, A.C. & Kemp (1998), Kemp, A.C. *et al.* (1988), Kemp, M. *et al.* (1989), Lewis & Pomeroy (1989), Lloyd (1997), Mackworth-Præd & Grant (1957, 1962, 1970), Maclean (1993), Marshall (1996), Mendelsohn (1989), Muhweezi & Butynski (1990), Nel (1969), Penry (1994), Perrett (1980), von Petersdorff (1991, 1992), Pickford *et al.* (1989), Pinto (1983), Porter, Christensen & Schiermacker-Hansen (1996), Rutgers & Norris (1972), Short *et al.* (1990), Skinner *et al.* (1980), Snow (1978), Steyn (1982, 1984, 1992, 1994c), Tilson & LeRoux (1984), Vernon (1980), Voous (1988), Woodhouse (1991), Zimmerman, D.A. *et al.* (1996).

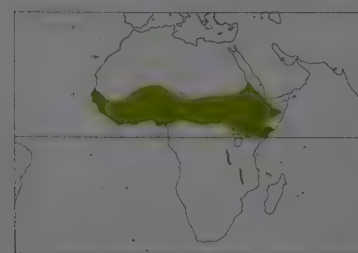
76. Greyish Eagle-owl

Bubo cinerascens

French: Grand-duc du Sahel **German:** Grauhuhu **Spanish:** Búho Ceniciento
Other common names: Vermiculated Eagle-owl

Taxonomy. *Bubo cinerascens* Guérin-Méneville, 1843, Adowa, Ethiopia. Usually treated as conspecific with *B. africanus*; differs, however, in plumage, bare-part colours, and not known to interbreed in overlap areas in Uganda and Kenya. Pale birds in Chad described as race *kollmannspergeri*, but probably only colour variant. Monotypic.

Distribution. Senegambia E to Ethiopia and Somalia, S to Cameroon, N Uganda and N Kenya.



Descriptive notes. c. 43 cm; c. 500 g. Relatively small eagle-owl, similar to *B. africanus*; compared with latter, has less spotting and more thin barring above, tail with narrower dark bars, browner below with very fine, dense dark vermiculations, and has greyish bill and dark brown rather than yellow eyes. Juvenile similar to *B. africanus*, but dark-eyed. **VOICE.** Male apparently gives loud 2-note hoot, second note deep and downslurred; differences from *B. africanus* unclear.

Habitat. Dry, rocky desert, semi-desert and hillsides with scattered trees and thorn scrub, and savanna with trees and bushes; in Somalia, also lowland woodland; avoids dense forest. In E of range, recorded visiting towns and suburbs.

Food and Feeding. Insects and other arthropods, small mammals and birds, reptiles and frogs. Nocturnal and crepuscular. Hunts from a perch, often beside road or track; probably also hawks aerial prey; recorded feeding on insects attracted to lights.

Breeding. Lays Nov–May in most of range; Aug in Nigeria, Mar–May in Somalia. Nest a scrape on ground on cliff ledge, sometimes in old tree nest of large bird. 1–3 eggs; incubation by female.

Movements. Resident; some local altitudinal movement to higher levels in hot summers.

Status and Conservation. Not globally threatened. CITES II. Generally rather uncommon throughout most of range. Uncommon in e.g. Senegambia, Uganda and Kenya; rare to uncommon in Liberia; fairly common in NW Somalia; thought to be common in Nigeria. In Sierra Leone, described as the commonest eagle-owl.

Bibliography. Ash & Miskell (1983b, 1998), Bannerman (1953), Barlow *et al.* (1997), Britton (1980), Cave & Macdonald (1955), Cheke & Walsh (1996), Colston & Curry-Lindahl (1986), Demeter (1981, 1982), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Elgood *et al.* (1994), Field (1998), Friedmann (1930), Fry *et al.* (1988), Gatter (1997), Giraudoux *et al.* (1988), Gore (1990), Green & Carroll (1991), Grimes (1987), Kemp & Kemp (1998), Lang (1969), Lewis & Pomeroy (1989), Mackworth-Præd & Grant (1957, 1970), Short *et al.* (1990), Snow, D.W. (1978, 1979), Steyn (1984), Voous (1988), Zimmerman, D.A. *et al.* (1996).

77. Fraser's Eagle-owl

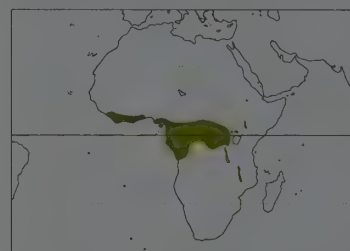
Bubo poensis

French: Grand-duc à aigrettes **German:** Guineahuhu **Spanish:** Búho de Guinea

Taxonomy. *Bubo Poensis* Fraser, 1853, Bioko (Fernando Póo).

May form superspecies with *B. vosseleri*. Sometimes treated as conspecific with latter, but geographical isolation and vocal differences, as well as differences in size and plumage, suggest distinct species. Monotypic.

Distribution. Liberia E to W Uganda, S through Congo basin to C Zaire and NW Angola; also Bioko (Fernando Póo).



Descriptive notes. 39–45 cm; male c. 575 g, female 685–815 g. Relatively small, with long ear-tufts; degree of rufous and extent of barring varies considerably among individuals. Facial disc pale rufous, edged in black; rufous with dark barring above, with pale scapular line; flight-feathers and tail narrowly barred with dusky and rufous; underparts pale rufous, fading to white on abdomen, all barred with black and rufous, chest with blotchy appearance; tarsus fully feathered; iris dark brown with pale blue eyelids; bill pale blue-grey. Juvenile pale whitish-rufous with thin dark bars, wings and tail as adult but much whiter.

scapulars; as adult by c. 1 year. **VOICE.** Loud purring trill, like sound of small engine; also drawn-out hooting "twowoooot", second part higher and more whistle-like, given every 3–4 seconds.

Habitat. Lowland evergreen and secondary forest, as well as forest edge and clearings; also plantations. Sea-level to 1600 m.

Food and Feeding. Insects, including beetles, grasshoppers, millipedes; also frogs and small birds, and small mammals such as mice, squirrels, fruit bats, tree hyraxes and small galagos; reports of occasional eating of fruit require corroboration. Nocturnal and crepuscular. Hunts mostly from perch.

Breeding. Poorly known; evidence suggests year-round laying, with no obvious seasonality; females with enlarged ovaries collected in Liberia in Jan, Sept, Nov, Dec; captive in Nigeria laid in Oct; nearly full-grown juveniles seen in Liberia in Jan and Aug. Nest possibly on ground or in tree hole; nestling found on ground, and another looking out of cavity. Details of clutch size, incubation and fledging period unknown; post-fledging dependence probably protracted, as juvenile does not moult mesopile plumage until 1 year old.

Movements. Apparently resident.

Status and Conservation. Not globally threatened. CITES II. Common in Liberia and Cameroon; uncommon in Sierra Leone. In Liberia, total of at least 5 pairs in 4 areas each of 1 km², and 5 birds calling along 10 km of road. Status elsewhere difficult to assess; biology relatively unknown, and breeding undocumented. Although suffers from forest degradation in many areas, will tolerate some habitat disturbance and readily adapts to secondary habitats and logged forest, so effects may be less severe than suspected. Occurs in several protected areas throughout its range, such as Gola Forest Reserve (Sierra Leone), Dzanga-Ndoki National Park and Dzanga-Sangha Rainforest Reserve (Central African Republic) and Impenetrable (Bwindi) Forest National Park (Uganda); recorded also at Mt Cameroon and Mt Kupé (Cameroon).

Bibliography. Bannerman (1953), Christy & Clarke (1994), Colston & Curry-Lindahl (1986), Dowsett (1989b, 1990), Dowsett & Dowsett-Lemaire (1991, 1993), Dowsett & Forbes-Watson (1993), Elgood *et al.* (1994), Field (1998), Fry *et al.* (1988), Gatter (1988, 1997), Green & Carroll (1991), Grimes (1987), Hall & Moerau (1962), Helsen (1996), Kemp & Kemp (1998), Lippens & Wille (1976), Louette (1981), Mackworth-Præd & Grant (1970), Pérez del Val (1996), Pinto (1983), Snow (1978).

78. Usambara Eagle-owl

Bubo vosseleri

French: Grand-duc des Usambara **German:** Usambarahuhu **Spanish:** Búho de Usambara
Other common names: Nduk Eagle-owl

Taxonomy. *Bubo vosseleri* Reichenow, 1908, Amani, Tanzania.

May form superspecies with *B. poensis*. Sometimes treated as subspecies of latter; species status based on apparent differences in vocalizations (and apparent lack of response to taped *B. poensis* call), size and plumage, and isolated range. Monotypic.

Distribution. Usambara Mts of NE Tanzania; recently discovered in Uluguru Mts; also possible sighting in Nguru Mts.

Descriptive notes. 48 cm; 770–875 g. Closely resembles *B. poensis*; differs in larger size, browner upperparts, whiter underside less regularly barred and with faint streaking, and heavier blotching on breast, and dull yellow-orange or orange-brown eyes. Juvenile with white-spotted scapulars forming distinct line across wing. **VOICE.** Low-pitched, weak "po-a-po-a-po-a-po-a", 5–7 seconds in duration.



tion, accelerating and then decelerating, dropping in pitch; each phrase repeated at intervals of 30-60 seconds, up to 4 times; given only at night; captives sometimes gave double note similar to that of *B. poensis*.

Habitat. Evergreen montane forest at 900-1500 m; also recorded at forested edge of tea plantations in lowlands, down to 200 m, where possibly more frequent.

Food and Feeding. No information; probably similar to *B. poensis*.

Breeding. Estimated laying period Oct-Feb; no other information.

Movements. Presumably resident; possible vertical movements to lower levels in cold weather.

Status and Conservation. VULNERABLE. CITES II. Restricted-range species; present in Tanzania-Malawi Mountains EBA. Following its discovery in 1908, not seen again until 1962. Scarcity may be attributable to its secretive and nocturnal habits. Population once thought to be no more than 200 birds, but increasing field work suggested more optimistic figure of 2 pairs/km², or nearly 500 pairs. Recent discovery of population in the Uluguru Mts indicates that, contrary to what was previously thought, it is unlikely that all breeding individuals are limited to a single subpopulation, and also that global

population size of species may be greater. Lowland areas with suitable habitat in Usambaras limited to c. 240 km². Forest clearance for subsistence farming, and cardamom and tea plantations, seen as a threat; cardamom, however, grown under intact canopy; several young birds found on ground in these cleared areas, so undisturbed forest perhaps not essential to species' survival. Nevertheless, conservation of forest, both montane and at lower levels, important; current projects designed to ensure survival, and even increase, of such habitat now under way.

Bibliography. Bennun & Njoroge (1996), Britton (1980), Britton *et al.* (1984), Brown (1977), Buckley & Matilya (1998), Clark & Mikkola (1989), Collar & Andrew (1988), Collar & Stuart (1985), Collar *et al.* (1994), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Evans, T.D. & Anderson (1992, 1993), Evans, T.D., Hague *et al.* (1994), Evans, T.D., Tye *et al.* (1997), Evans, T.D., Watson *et al.* (1994), Fry *et al.* (1988), Hipkiss *et al.* (1994), Hunter *et al.* (1996), Kemp & Kemp (1998), King (1978/79), Mackworth-Praed & Grant (1957), Moreau (1964), Olney (1984), Seddon *et al.* (1999), Short *et al.* (1990), Shuker (1993), Snow (1978), Stattersfield *et al.* (1998), Stuart & Hutton (1977), Stuart & Turner (1980), Stuart & van der Willigen (1978), Turner *et al.* (1991), Waiyaki (1996), White, G.B. (1974), Zimmerman, D.A. *et al.* (1996).



79

80

81

82

83



86



84



85



88



89



87

ssp semenowi

ssp zeylonensis



91



92



93



90

♂

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PLATE 11

inches 10
cm 25

79. Forest Eagle-owl

Bubo nipalensis

French: Grand-duc du Népal

German: Nepaluhu

Spanish: Búho Nepali

Other common names: Spot-bellied Eagle-owl

Taxonomy. *Bubo nipalensis* Hodgson, 1836, Nepal.

Possibly forms superspecies with *B. sumatranus*. Two subspecies recognized.

Subspecies and Distribution.

B. n. nipalensis Hodgson, 1836 - Himalayas from N Uttar Pradesh E to SW China (Yunnan), S to Cambodia and Vietnam; also S India in Western Ghats and Tamil Nadu.

B. n. blighi Legge, 1878 - Sri Lanka.

Descriptive notes. 51-64 cm. Large, powerful, dark brown owl, with well-developed, outward-slanting ear-tufts composed of feathers of different sizes. Facial disc whitish; dark brown above, mottled and barred with buffy-white; below, buffy-white, barred with blackish on throat and breast, with dark brown v-shaped spots on lower breast and abdomen; tarsus fully feathered; iris brown to hazel-brown; bill dull wax-yellow to yellow; feet dusky yellow. Juvenile conspicuously pale, buff to whitish, narrowly barred above and below; moults into adult plumage at 1 year. Race *blighi* smaller, darker above, less barred below. **Voice.** Deep, low, resounding "hoo hoo", 2 seconds between notes; also loud, mournful scream with rising and falling rhythm.

Habitat. Dense evergreen and moist deciduous forest, usually near water, montane wet temperate forest, and dense riparian gallery forest; hunts also in scrub, bamboo jungle, thin deciduous forest, sometimes edges of clearings. From 300 m to 2130 m, locally to 3000 m in Himalayas.

Food and Feeding. Mainly large birds; also mammals, and reptiles and fish; occasionally carrion. Bird prey include large phasianids, especially junglefowl, peafowl and pheasants, e.g. Kalij Pheasant (*Lophura leucomelanos*); mammals include hares, jackals, barking-deer fawns; monitor lizards sometimes taken. Mostly nocturnal; occasionally hunts during day. Bold and powerful hunter; hunts from perch, or pounces on roosting birds or other prey.

Breeding. Lays Feb-Mar in Himalayas and Nepal; Dec-Jan in S India; Apr-May in Sri Lanka. Nest in large tree cavity or abandoned nest of raptor; also lays on bare soil in cave or sheltered fissure in rock wall. Usually 1 egg; reported to be fierce in defence of eggs or nestlings.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Currently considered Near-threatened. Rare and local in Indian Subcontinent, including Sri Lanka; at best uncommon in Thailand; rare to very rare in other parts of range; in Myanmar, reported to be well distributed but much overlooked. Appears to be dependent on continued existence of tropical lowland and hill forest, habitat under severe pressure throughout S Asia; no indication of ability to colonize degraded areas.

Bibliography. Ali (1996), Ali & Ripley (1981), Ali *et al.* (1996), Brack (1996), Daniels (1997), Deignan (1945), Delacour & Jabouille (1940), Duckworth *et al.* (1998), Gokula & Vijayan (1997), Grimmett *et al.* (1998), Henry (1998), Inskipp & Inskipp (1991), Lamsfuss (1998), Lekagul & Round (1991), Majumdar *et al.* (1992), Neelakantan (1965), Riley (1938), Ripley (1982), Smythies (1986), Thewlis *et al.* (1998), Voous (1988), Wang Sung (1998), Zhao Zhengjie (1995).

80. Barred Eagle-owl

Bubo sumatranus

French: Grand-duc bruyant

German: Malaieuhu

Spanish: Búho Malayo

Other common names: Malay/Malaysian Eagle-owl

Taxonomy. *Strix Sumatrana* Raffles, 1822, Sumatra.

Possibly forms superspecies with *B. nipalensis*. Suggested that it may have some morphological and vocal affinities with African *B. shelleyi*. Bornean population sometimes separated racially (as *tenuifasciatus*). Two subspecies recognized.

Subspecies and Distribution.

B. s. sumatranus (Raffles, 1822) - extreme S Myanmar and peninsular Thailand S to Sumatra, including Bangka I.

B. s. strepitans (Temminck, 1823) - Borneo, Java and Bali.

Descriptive notes. 40-46 cm. Relatively small eagle-owl with long, outward-directed ear-tufts. Facial area dirty whitish, ear-tufts dark brown, finely marked with white; blackish-brown above, barred with rufous-buff, some buff-white on scapulars; flight-feathers and tail widely barred; greyish-white below, tinged rufous-brown on chest, and barred with brown; tarsus fully feathered; iris dark brown; bill and feet yellow. Juvenile buffy-white, barred with dark brown. Race *strepitans* larger, barring below stronger and denser; Bornean birds somewhat intermediate. **Voice.** Loud "whoa-who, whoa-who", ending with deep groan,

each hoot with downward inflection; also various shrieks and cackles.

Habitat. Lowland evergreen forest and semi-evergreen forest, and forest edge and clearings; also secondary growth and old plantations, and well-wooded gardens. Mostly from lowlands to 600 m, locally to 1000 m; in Malay Peninsula recorded exceptionally to 1400 m, and in Java to 1600 m.

Food and Feeding. Diet includes large insects, as well as small mammals, especially rodents, and snakes and small birds; probably takes some larger prey, too. Nocturnal and crepuscular. Hunts from perch, and hops well on ground; flies fast and low from diurnal roost at dusk.

Breeding. In Peninsular Malaysia, fledglings found in Jan, late Feb and Apr-Jun; in Sumatra, nestlings and young fledglings in Mar-May; in Borneo, young in Feb-Mar, reported to breed before rice

harvest; in Java, eggs in Feb-Apr, chicks in May-Jun. Nest in tree cavity; in Sumatra and Java, often on bird's-nest fern (*Asplenium nidus*). Usually 1 egg; incubation and fledging periods unknown.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Little information available. Uncommon in Thailand; uncommon to fairly common in Peninsular Malaysia; sparingly distributed throughout Borneo; locally fairly common in other parts of range. Ability to adapt to disturbed forest and to accept second-growth habitats suggests that species is not in any immediate danger.

Bibliography. Andrew (1992), Delacour (1947), Glenister (1951), Hellebrekers & Hoogerwerf (1967), Hoogerwerf (1949a), Holmes (1996), Lekagul & Round (1991), MacKinnon (1988), MacKinnon & Philipps (1993), van Marle & Voous (1988), Medway & Wells (1976), Meyer de Schauensee & Ripley (1940), Nash, S.V. & Nash (1985, 1988), Smythies (1981, 1986), Tobias (1995), Vowles & Vowles (1984), Wells (1999).

81. Shelley's Eagle-owl

Bubo shelleyi

French: Grand-duc de Shelley

German: Bindenuhu

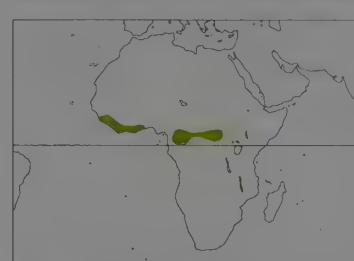
Spanish: Búho Barrado

Other common names: Banded Eagle-owl

Taxonomy. *Huhua shelleyi* Sharpe and Ussher, 1872, Fantee, Ghana.

No obvious close relatives; may possibly have some vocal and morphological affinities with *B. sumatranus* of SE Asia. Monotypic.

Distribution. Sierra Leone and Liberia E to Ghana, and S Cameroon and N Gabon E to N Zaire.



Descriptive notes. c. 61 cm; 1 male 1257 g. Big, dark, heavily barred eagle-owl with "tousled" brown ear-tufts. Facial disc creamy to tawny with dusky bars, edged in black; head dusky brown with few white feathers on nape; upperparts dark brown with dark buff bars; flight-feathers and tail barred dusky and dark buff; breast and belly cream to white with bold, broad dusky bars; tarsus fully feathered, toes pale cream; iris dark brown; bill dull yellow. Juvenile has large areas of white on head, with sooty barring. **Voice.** Loud, wailing "kooouu", given irregularly at intervals of some seconds; continuous soft peeping when stressed.

Habitat. Lowland primary rainforest and forest edge.

Food and Feeding. Virtually nothing known; observed eating large flying squirrel. Large size and powerful feet suggest that variety of mid-sized to large prey taken. Captive bird required c. 110 g of flesh per day.

Breeding. In Liberia, intense calling in Mar; in Cameroon, adult roosting with possible juvenile in Dec; in Zaire, large nestling found in Sept, nestling in mesoptile plumage early Nov, and fledged young in Dec. No other information.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Rare and very local throughout its range. Reported as rare to uncommon in Liberia. Known from only 1 record in Sierra Leone. One of the least-known of African owls; breeding and general ecology almost undocumented. Owing to its rarity and fragmented distribution, and poorly documented biology, conclusive comments on its status difficult. Conservation status probably merits reappraisal.

Bibliography. Bannerman (1953), Chapin (1960), Colston & Curry-Lindahl (1986), Dowsett (1989b), Dowsett & Dowsett-Lemaire (1991, 1993), Dowsett & Forbes-Watson (1993), Field (1998), Fry *et al.* (1988), Gartshore (1989), Gatter (1988, 1997), Grimes (1987), Kemp & Kemp (1998), Lippens & Wille (1976), Louette (1981), Mackworth-Præd & Grant (1970), de Roo (1966a), Schouteden (1966), Snow (1978), Thiollay (1985).

82. Verreaux's Eagle-owl

Bubo lacteus

French: Grand-duc de Verreaux

German: Blaßuhu

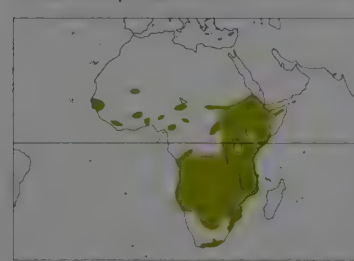
Spanish: Búho Lechoso

Other common names: Giant/Milky Eagle-owl

Taxonomy. *Strix lactea* Temminck, 1820, Senegal.

No close relatives. Monotypic.

Distribution. Tropical W Africa patchily from Senegal and C Mali E to Cameroon, and from C Sudan, N Ethiopia and Somalia S to South Africa.



Descriptive notes. 60-65 cm; wingspan 140 cm; male 1615-1660 g, female 2475-3115 g. Largest African owl; distinct dusky ear-tufts. Off-white facial disc rimmed in black; upperparts grey-brown, scapulars and wing-coverts with some white; flight-feathers and tail barred dusky and light brown; underparts whitish with fine dark grey-brown vermiculations, darkest on upper breast; tarsus and toes fully feathered; iris brown, with conspicuous pink eyelids; bill pale horn, with black bristles at base. Juvenile has body and head grey-brown with broad bars, facial disc less pronounced, smaller ear-tufts. **Voice.** Deep, grunting "gwok gwok" notes,

uttered in uneven series of 1-5 hoots, may carry up to 5 km; also whining calls.

Habitat. Open thorny savanna and semi-desert with scattered trees; riparian areas with stands of large trees, often adjoining savanna; also small forest patches, open woodland, tall moist woodland and stands of exotic trees; absent only from dense forest and bare desert. In W Africa, appears to prefer riparian habitat. From sea-level to 3000 m.

Food and Feeding. Opportunistic, diet based on prey availability. Mostly medium-sized mammals and larger birds; also reptiles, amphibians, fish, insects, spiders and scorpions, and carrion. Diversity of mammal prey, from young monkeys, warthog piglets, mongooses and hyraxes to fruit bats,

cane rats and gerbils; birds from estrildids and other passerines up to ducks, Black-headed Heron (*Ardea melanocephala*), Secretarybird (*Sagittarius serpentarius*) and other raptors; excessively mobbed by birds if disturbed from daytime roost. Only major predator of South African hedgehogs (*Aterix*), leaving characteristically peeled pelts uneaten. At SW limit of range, birds, especially herons, most important. Requires c. 5% of body weight in food per day. Sometimes caches excess food. Rarely drinks. Crepuscular and nocturnal, but records of killing animals that pass beneath its roost during day; inquisitive, attracted to any commotion. Hunts from perch, gliding down to capture prey, killing it with its heavy feet and long talons along with impact of the blow; occasionally flushes prey in low searching flight. Also crashes into foliage after roosting birds or arboreal mammals; runs on ground, wades into water after fish; hawks flying insects, seizing these with its feet.

Breeding. Lays Mar-Sept, peak in Jun-Aug; Jan-Mar in W, Oct-Jan in NE. Monogamous. Uses old stick nest of other bird such as eagle, vulture, Secretarybird, Hamerkop (*Scopus umbretta*) or corvid, or uses nest colony of weavers (*Bubalornis*, *Philetaurus*) as platform; sometimes on ground, e.g. beneath hollowed-out roots of tree; occasionally lays in cavity or tree hollow; may usurp nests of smaller species; often same site used yearly; average territory size c. 7000 ha. 1-2 eggs; incubation 32-39 days, by female, fed by male; chicks hatch asynchronously with up to 7-day interval, younger either starves or is killed by sibling, occasionally both raised; chick with creamy-white down, brooded up to c. 20 days by female, male provides food and transfers it to female, who feeds chick; young leaves nest before able to fly, fledges within following 2 weeks at 62-63 days, hides and remains inactive until c. 3 months old, depending on parents for food; juvenile sometimes stays with parents for 2 years and helps raise next brood. Pair at E Cape raised a chick in 4 successive years. First breeding at 3-4 years old; annually thereafter, or irregularly at intervals of 2-4 years, probably related to prey abundance but exact factors unknown. Captive individual survived 15 years.

Movements. Resident, even in arid areas; only local dispersal of young.

Status and Conservation. Not globally threatened. CITES II. Common and widespread throughout most of its range; generally less common in W, where also more local. Common in Senegambia, but considered uncommon in Sierra Leone, and rare in Liberia, Ghana and Cameroon; recent observations suggest possibly quite common in Benin; species may be overlooked in areas where it prefers riparian habitat, as in W Africa. Few records from W & SE Tanzania, N Kenya or coastal regions of E. Able to survive in wide range of habitats, and adaptable, so not vulnerable to forest clearance. Main threat probably human persecution.

Bibliography. Agutu (1994), Ash & Miskell (1998), Avery *et al.* (1985), Bannerman (1953), Barlow *et al.* (1997), Benson & Benson (1977), Benson *et al.* (1971), Boshoff (1987, 1996), Brown (1965), Bursell (1992), Cave & Macdonald (1955), Cheke & Walsh (1996), Claffey (1998), Colston & Curry-Lindahl (1986), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Dugmore (1997), Elgood *et al.* (1994), Field (1998), Friedmann (1930), Fry *et al.* (1988), Gatter (1997), Ginn *et al.* (1989), Giraudoux *et al.* (1988), Gore (1990), Grimes (1987), Hammer (1981), Harrison *et al.* (1997), Herholdt (1993a), Ives (1991), Kemp & Calburn (1987), Kemp & Kemp (1998), Lewis & Pomeroy (1989), Mackworth-Præd & Grant (1957, 1962, 1970), Maclean (1993), Penny (1994), Pickford *et al.* (1989), Pinto (1983), Pitman & Adamson (1978), Schwab & Wright (1990), Short *et al.* (1990), Smart & Taylor (1990), Snow, D.W. (1978, 1979), Steyn (1982, 1984, 1994c), Vernon (1980), Wilson & Wilson (1981), Zimmerman, D.A. *et al.* (1996).

83. Dusky Eagle-owl

Bubo coromandus

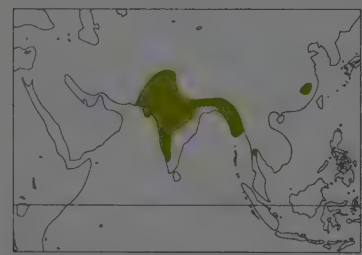
French: Grand-duc de Coromandel **German:** Koromandeluhu **Spanish:** Búho de Coromandel
Other common names: Dusky Horned Owl

Taxonomy. *Strix coromanda* Latham, 1790, Coromandel Coast.
No obvious close relatives. Two subspecies recognized.

Subspecies and Distribution.

B. c. coromandus (Latham, 1790) - Pakistan, N & C India and S Nepal E to Assam and Bangladesh; apparently this race also in E China.

B. c. klossi Robinson, 1911 - W & S Myanmar, W Thailand.



Descriptive notes. 48-53 cm. Large, greyish owl with prominent ear-tufts rounded at tips. Pale facial disc framed by narrow black lines; above, dark brown with greyish tinge, obscurely marked with long, narrow, widely spaced streaks of dark brown, and buffy-white spots on wing-coverts; tail dark brown, barred, paler at tip; below, very pale buffish-grey with narrow black streaks; tarsus fully feathered; iris yellow; bill greyish-white, tip pale yellowish-horn; feet pale grey-brown. Juvenile mostly rufous, with greyer head. Race *klossi* darker, more brown. **VOICE.** Accelerating "wo wo wo wo-wo-wowowo", becoming softer with each note; low, deep rumbling "woo-woo-woo"; loud, piercing call; calls during day or night.

Habitat. Open, level areas with plenty of woodland, generally near water; riparian forest, old plantations, e.g. of mango, thickly foliated groves and roadside trees; has adapted to irrigated forest plantations. Lowlands, to c. 250 m.

Food and Feeding. Birds, especially crows (*Corvus*), but ranging from pigeons and doves, parakeets, coucals (*Centropus*) and coraciiforms to hawks, and waterbirds such as waders, coots (*Fulica*) and pond-herons (*Ardeola*); also small to medium-sized mammals, such as rats, hares and squirrels, and porcupine recorded as prey; also takes reptiles and amphibians, and fish; insects also recorded, mainly water beetles (*Dytiscus*), and birds' eggs. Semi-diurnal; quite often active during daylight, especially in dull weather. Hunting methods poorly documented; hunts from perch, probably also in searching flight, and on ground, and wades in shallow water, catches birds as they fly in to roosts. Decapitates large prey before taking to feeding perch or nest.

Breeding. Lays late Nov-Apr, mainly Dec-Jan, later in S; fledglings found from early Feb. Lays in old stick nest of raptor, commonly kite, vulture or eagle, high up in tree fork; record of ground nesting in Bombay; reports of occasionally building own nest, or lining old one with greenery, unconfirmed, highly doubtful. Usually 2 eggs, sometimes 1 or 3; incubation by both sexes reported, period unknown; eggs hatch asynchronously, usually only older, stronger nestling reaches maturity; chick with white down; fledging period and dependence unrecorded.

Movements. Resident; old records from Peninsular Malaysia presumed to have involved vagrants, but no evidence of any regular movements.

Status and Conservation. Not globally threatened. CITES II. Little information. Widespread but uncommon in India, more frequent in Pakistan, local and rare in Nepal and Bangladesh. Said to be fairly common in Myanmar, at least formerly, but current status there not known; status in Thailand unclear, apparently extremely rare, only handful of records ever, none of breeding, and possibly only winter visitor or vagrant; only 4 records from Peninsular Malaysia, last in 1915, considered to

have involved vagrants from farther N. Possible that range of race *klossi* has contracted, thus explaining paucity of modern records in well-watched regions; indeed, current evidence indicates that population at very low level, perhaps threatened. Chinese population of nominate race virtually unknown; requires further investigation.

Bibliography. Ali (1996), Ali & Ripley (1981), Daniels (1997), Eates (1939), Grimmett *et al.* (1998), Inskipp & Inskipp (1991), Lekagul & Round (1991), Mahabal & Lamba (1987), Medway & Wells (1976), Mirza (1985), Mukherjee (1995), Ripley (1982), Roberts (1991), Round (1988), Smythies (1986), Thompson *et al.* (1993), Wang Sung (1998), Wells (1999), Zhao Zhengjie (1995).

84. Akun Eagle-owl

Bubo leucostictus

French: Grand-duc tacheté **German:** Schwachschnabeluhu **Spanish:** Búho de Akún
Other common names: Sooty Eagle-owl

Taxonomy. *Bubo leucostictus* Hartlaub, 1855, Dabocrom, Ghana.

No obvious close relatives. Monotypic.

Distribution. Patchily from Sierra Leone and Liberia E to Nigeria and Cameroon, S to mouth of R Congo, Cabinda and probably NW Angola, and across N Zaire.



Descriptive notes. 40-46 cm; male 485-535 g, female 525-610 g. Relatively small eagle-owl, with comparatively small feet and weak bill. Facial disc light rufous with pale rings, dark rim; head and ear-tufts dark brown with white spots; upperparts, including flight-feathers, brown to rufous-brown with pale dusky brown bars, scapulars with white outer webs; tail banded, with conspicuous white tip; throat white; breast light rufous-brown, spotted and barred dark, rest of underparts white with thin rufous vermiculations and large blackish spots; tarsus feathered; iris pale yellow; bill greenish-yellow. Juvenile has head and body whitish with rufous barring, contrasting brown wings and tail; as adult at 1 year. **VOICE.** Low, accelerating clucking rattle, "tok tok tok-ok-ok-ok", given infrequently; quacks in alarm.

Habitat. Primary and secondary lowland rainforest, mainly at edges and clearings; also forest along rivers and forested river islands; in Liberia, recorded also in swampy areas of virgin forest and in farmland areas with tall trees.

Food and Feeding. Mainly insects, such as beetles, cicadas and locusts; vertebrates not recorded in diet; captive birds refused larger rodents, but ate oil-palm fruit; small feet and weak bill suggest incapable of overpowering large birds or mammals. Nocturnal, emerging at dusk. Hunts from perch in middle storey, often near clearing or track; flies low down along roads and open trails. Seizes prey from foliage or the ground; also catches insects on wing, observed hawking cockroaches at dusk. Food held in foot, and broken into pieces by nipping with bill.

Breeding. Gonadal condition of specimens indicates laying in Nov-Dec in Sierra Leone, Nov-Jan in Gabon, and Mar and Aug-Sept in Zaire; in Liberia, nestlings in Feb-Apr and juvenile in Jul. Nest apparently on ground. No other information.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Patchy distribution with restricted pattern of occurrence; usually considered uncommon. Uncommon in Sierra Leone, and thought rare in Nigeria; found to be common in Liberia, with up to 1 pair/km² in NW. Although poorly known, and breeding more or less undocumented, species is easily overlooked; possibly more common than records suggest. More study needed to assess its status, and any possible impacts of logging.

Bibliography. Bannerman (1953), Colston & Curry-Lindahl (1986), Dowsett & Dowsett-Lemaire (1991, 1993), Dowsett & Forbes-Watson (1993), Dowsett *et al.* (1999), Elgood *et al.* (1994), Field (1998), Fry *et al.* (1988), Gatter (1988), Green & Rodewald (1996), Grimes (1987), Jellicoe (1954), Kemp & Kemp (1998), Lippens & Wille (1976), Louette (1981), Mackworth-Præd & Grant (1970), Pinto (1983), Snow (1978), Stephenson & Newby (1997), Thiollay (1985).

85. Philippine Eagle-owl

Bubo philippensis

French: Grand-duc des Philippines **German:** Streifenuhu **Spanish:** Búho Filipino
Other common names: Philippine Horned Owl

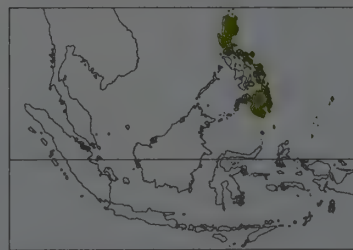
Taxonomy. *Pseudopteryx philippensis* Kaup, 1851, Philippines.

No obvious close relatives. Two subspecies recognized.

Subspecies and Distribution.

B. p. philippensis (Kaup, 1851) - Luzon and Catanduanes.

B. p. mindanensis (Ogilvie-Grant, 1906) - Samar, Leyte and Mindanao; recently recorded on Bohol.



Descriptive notes. 40 cm. Smallish, rufous eagle-owl with small, outward-slanting ear-tufts. Facial disc rufous-buff; head, breast and upperparts tawny-rufous with broad dark brown stripes; wings and tail barred dark brown and rufous-buff; upper throat unstreaked buff; lower breast to belly buffy-white, streaked dark brown; tarsi feathered to base of toes; iris yellow; bill bluish-horn; toes bluish to flesh-coloured. Juvenile undescribed. Race *mindanensis* darker, more heavily streaked. **VOICE.** Uncertain, confused with other Asian forest owls.

Habitat. Forest, often near rivers or lakes;

occurs at lower elevations.

Food and Feeding. No information; large and powerful feet suggest that diet composed of small mammals or birds.

Breeding. No information.

Movements. Resident.

Status and Conservation. ENDANGERED. CITES II. Rare; very few recent records, all from Luzon, except for unexpected sighting in 1994 on Bohol, where previously unrecorded. Rapid population decline due to extensive lowland habitat destruction, and possibly hunting. The pres-

ence of more than 10 individuals kept in Manila Zoo in 1994 would seem to indicate that species may be locally less rare than scarcity of records suggests.

Bibliography. Anon. (1997b), Brooks & Dutton (1997), Brooks *et al.* (1996), Collar *et al.* (1994), Danielsen *et al.* (1994), Delacour & Mayr (1946), Dickinson *et al.* (1991), Heaney & Regalado (1998), Oliver & Wirth (1996), Gogorza y González (1987), Gonzales (1983), McGregor (1909-1910, 1921), Ogilvie-Grant (1894), Parkes (1973), duPont (1971), Poulsen (1995), Rabor (1938a), Rand & Rabor (1960), Whitehead (1899).

86. Blakiston's Eagle-owl

Bubo blakistoni

French: Grand-duc de Blakiston **German:** Riesenfischuhu **Spanish:** Búho Manchú
Other common names: Blakiston's Fish-owl

Taxonomy. *Bubo blakistoni* Seebohm, 1884, Hokkaido, Japan.

Sometimes placed in genus *Ketupa*, and has been treated as forming superspecies with, or even conspecific with, *K. zeylonensis*. Skeletal details, however, especially skull morphology, appear identical to those of *Bubo* (e.g. *B. bubo*) and different from osteology of *Ketupa*. Four subspecies recognized.

Subspecies and Distribution.

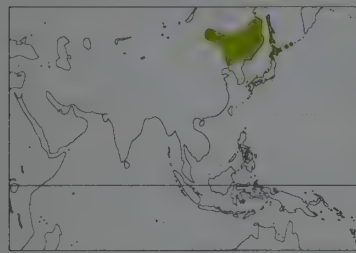
B. b. piscivorus Meise, 1933 - W Manchuria (W of Great Khingan Mts).

B. b. doerriesi Seebohm, 1895 - SE Siberia and extreme NE China, to Korean border.

B. b. karafutonis Kuroda, 1931 - Sakhalin I.

B. b. blakistoni Seebohm, 1884 - Hokkaido and S Kuril Is.

Descriptive notes. 60-72 cm; wingspan 180-190 cm. One of largest of all owls; ear-tufts broad, long, horizontal. Facial disc pale grey-brown; upperparts buff-brown, broadly streaked, wings barred buff and dark brown; tail almost white, barred dark; white throat; below, pale buffish-brown with long, thin streaks; tarsi feathered almost to base of toes; iris orange-yellow; bill pale grey-horn, yellowish at tip; toes dark brown-grey. Juvenile with spots and whitish feather edgings above. *Race doerriesi* larger, with white crown patch; *piscivorus* paler; *karafutonis* smaller and darker than nominate, tail more narrowly barred. **VOICE.** Territorial call short, deep



"boo-bo-boo" or "shoo-hoo"; elaborate duets; begging call long, slurred "peer-peer-peer".

Habitat. Dense broadleaf or mixed broadleaf/coniferous forest along clear rivers, favouring tributary confluences where some slow-flowing channels; steep-sided wooded valleys near fast-flowing rivers; also taiga rivers which do not freeze in winter; in Kurils, dense conifer forest adjacent to water, including sea coast. Also forages on rocky coasts. Lowlands.

Food and Feeding. Primarily fish, including large ones; also crabs, crayfish, frogs, and birds up to size of grouse (Tetraonidae); occasionally bats in flight. In autumn and winter, diet includes many crayfish, other crustaceans, as well as small mammals; sometimes cats and small dogs. Forages mainly at night (fish) or dusk (frogs); also by day. Hunts from low branch, log or bank overlooking river shallows; often walks about on ground, occasionally stands in water; jumps on prey and kills with talons; sometimes swoops to catch fish near surface, or dives feet first into deep water. In winter, will wait by air holes in ice; sometimes up to 5-6 individuals together.

Breeding. Lays late Feb-mid Mar, when snow cover still deep. Probably pairs for life. Nest a spacious hole up to 18 m above ground in large hollow tree, or in nestbox, or in fallen tree, sometimes on ground in forest; highly territorial, in Siberia territory covering 6-12 km of river valley. Courtship feeding begins 4 days before first copulation; most copulations around sunset. Usually 2 eggs (1-3); incubation 35-37 days, by female, fed on nest 3-5 times nightly by male; female leaves only to defecate and preen, travelling no more than 100 m from nest; chick with white down; young leave nest at 35-40 days, remain with parents for several months; juveniles sometimes dependent on adults for up to 1 year, especially during harsh winters. Apparently breeds only in alternate years. Lifespan probably 20 years or more.

Movements. Resident.

Status and Conservation. **ENDANGERED.** CITES II. One of world's rarest owls. Numbers in Russia, including Sakhalin and S Kuril Is. estimated at 300-400 pairs in 1984; formerly present throughout Hokkaido (Japan), but now confined to E & C parts, where 80-100 birds estimated in late 1980's, with only c. 20 pairs breeding in any year; in NE China extremely rare and local, possibly now extinct. Has declined massively over entire range, especially since 1950's; on R Bikin, in Ussuriland, decrease from estimated 70 birds (26 pairs) in mid 1970's to current total of 15 pairs or fewer. Main threats are development of riverside habitats and deforestation, especially destruction of taiga forest in Far East and Japan; on lower R Bikin, human population pressure forcing it to move to less productive rivers. Depletion of fish stocks through overfishing also an adverse factor. Furthermore, this species' habit of concentrating around fishing holes in Siberia renders it vulnerable to hunters and fishermen; also persecuted by fur-trappers, and sometimes dies in traps set for mink; hunted for food locally in Siberia. Provision of nestboxes has achieved some success on Kunashiri I and Hokkaido, where pairs have bred in these artificial nests annually since 1983. Attempts at captive-breeding unsuccessful.

Bibliography. Berezan (1993), Borodin (1984), Brazil (1985, 1989, 1991), Brazil & Yamamoto (1989a, 1989b), Cheng Tsohsin (1987), Clark & Mikkola (1989), Collar & Andrew (1988), Collar *et al.* (1994), Dykhan & Kiseleiko (1988), Échécoar & Hùe (1978), Flint *et al.* (1984), Hayashi (1997), Knystautas (1993), Mikhailov & Shibeve (1998), Nechaev (1991), Pukinsky (1973, 1974), Sasaki & Fujimaki (1995), Spangenberg (1965), Stepanyan (1990), Voous (1988), Yamamoto (1994), Yanagawa (1993), Zhao Zhengjie (1995).

Genus KETUPA Lesson, 1830

87. Brown Fish-owl

Ketupa zeylonensis

French: Kétoupa brun **German:** Fischuhu **Spanish:** Búho Pescador de Ceilán
Other common names: Ceylon Fish-owl, Brown Fishing-owl

Taxonomy. *Strix zeylonensis* J. F. Gmelin, 1788, Sri Lanka.

Genus *Ketupa* sometimes merged with *Bubo*, or treated as a subgenus. Present species then considered by some authors as forming superspecies with, or even conspecific with, *B. blakistoni*, but skeletal details, especially skull osteology, of latter appear identical to those of *Bubo* (e.g. *B. bubo*) and unlike *Ketupa*. Four subspecies recognized.

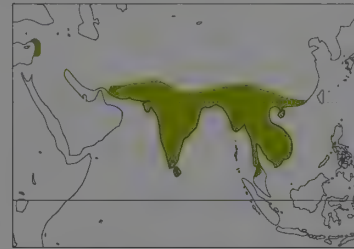
Subspecies and Distribution.

K. z. semenowi Zarudny, 1905 - S Turkey, Israel (probably extinct) and N Syria to NW India.

K. z. leschenaulti (Temminck, 1820) - India (S of Himalayas) E to Myanmar (except NE) and Thailand.

K. z. zeylonensis (J. F. Gmelin, 1788) - Sri Lanka.

K. z. orientalis Delacour, 1926 - NE Myanmar to SE China (Guangxi, Guangdong), S to Malay Peninsula, Indochina and Hainan I.



Descriptive notes. 50-57 cm; c. 1105 g. Large, flat-headed owl, with noticeable ear-tufts usually held horizontally. Facial disc buff, with dark brown upper cheeks; crown and upperparts pale chestnut with dark brown mottling and streaking; wing-coverts and flight-feathers dark brown, mottled with whitish-buff; tail barred brown and buff; throat white; underparts buffish-white with dark shaft streaks and thin rufous cross-lines; tarsus unfeathered; iris bright yellow; bill green-grey, tip darker; legs and feet yellowish. Juvenile less mottled, more narrowly streaked. *Race leschenaulti* larger and paler than nominate; *orientalis* darker, with

more black above, stronger buff below; *semenowi* very pale, brighter-coloured. **VOICE.** Deep, hollow, humming "boom boom" or "boo o-boom", repeated at intervals; also more muted "hu-who-hu".

Habitat. Deciduous, semi-deciduous and open evergreen woodland, well-vegetated ravines, steep banks and canalsides, old plantations and groves with mature trees, almost always near water; in Middle East, occupies undisturbed wadis and valleys with trees and bushes in hilly areas; streamside forest in China. Lowlands and foothills, to c. 1500 m; in Thailand, from plains up to 800 m; in China, at 600-1900 m.

Food and Feeding. Mainly fish, frogs and freshwater crabs; also crayfish, snakes and lizards, occasionally rodents and birds; also insects, e.g. large beetles. Occasional records of feeding on carrion; observed feeding on crocodile carcass. Nocturnal and crepuscular, often diurnal. Hunts from perch overlooking water; swoops down and dangles legs in water, seizing prey in talons; also wades after food.

Breeding. Lays Nov-May in Indian Subcontinent, mostly Jan-Feb in N. Apr in Sri Lanka; eggs in Dec in Malay Peninsula; breeds in dry monsoon season when water levels low and fish easily located. Presumed to pair for life. Nest in hollow or suitable depression in tree, or in old raptor nest, or on rock ledge or steep stream bank, usually near water, recorded at 4-21 m above ground; in India, sometimes on ruined building. Usually 2 eggs (1-3); incubation 34-38 days, by female; reports of male assisting incubation unconfirmed, highly improbable; fledging c. 51 days.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Generally uncommon. Apparently more numerous in Sri Lanka, where said to be possibly one of commonest strigids; local in Bangladesh, and local and uncommon in E of range. Rare in W of range; in Middle East, either extinct or on the verge, with last confirmed sighting in mid 1970's, and none located in surveys in mid 1980's; 1 substantiated record in S Turkey in 1990; extirpation in Israel thought to be result of mass poisoning of rodents in 1950's by agricultural chemicals, as well as draining of L Hula and adjacent swamp, and pollution of rivers; possibly survives in N Syria, perhaps also SE Iraq; almost certainly extinct in N Israel and S Syria. Doubtful if any remain in Iran, and very rare in Pakistan.

Bibliography. Ali (1996), Ali & Ripley (1981), Beaman & Madge (1998), Busch (1986), Cramp (1985), Deignan (1945), Échécoar & Hùe (1978), Evans (1994), Gregson (1986), Grimmett *et al.* (1998), Hùe & Échécoar (1970), Inskipp & Inskipp (1991), Lekagul & Round (1991), Magnin (1991), Medway & Wells (1976), Mendelsohn (1996), Mikkola (1983), Mukherjee (1995), Paz (1987), Phillips (1978), Porter, Christensen & Schiormacker-Hansen (1996), Ripley (1982), Roberts (1991), Rooke (1998), Schluter (1987, 1988), Shirihai (1996), Smythies (1986), Snow & Perrins (1998), Turnbull (1988), Voous (1988), Wells (1999), Zhao Zhengjie (1995).

88. Tawny Fish-owl

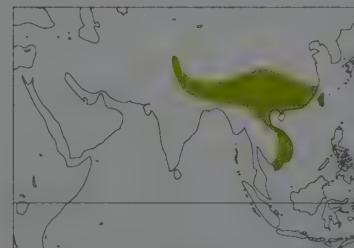
Ketupa flavipes

French: Kétoupa roux **German:** Himalayafischuhu **Spanish:** Búho Pescador Leonado

Taxonomy. *Cultrungius Flavipes* Hodgson, 1836, Nepal.

Genus *Ketupa* sometimes merged with *Bubo*, or treated as a subgenus; separated on basis of slight differences in skull morphology. Probably forms superspecies with *K. ketupa*, the two replacing each other geographically. Monotypic.

Distribution. Himalayas from NW India, Nepal and Bhutan to NE India, E to C China and Taiwan, and S to N Bangladesh, NE Myanmar and S Indochina.



Descriptive notes. 48-55 cm. Large fish-owl with prominent horizontal ear-tufts. Facial disc orange-rufous with indistinct dark border; above, rich orange-rufous or tawny with broad blackish shaft streaks, scapulars and wing-coverts with much buffy colour; flight-feathers barred dark brown; tail dark brown, barred buffy; usually well-defined white throat patch; below, orange-rufous with dark brown shaft streaks, broadest on breast; tarsi feathered for half way or more at front; iris yellow; bill horn-black, sometimes yellowish at tip; feet yellowish-grey or slaty-green. Distinguished from *K. ketupa* by larger size, feathered tarsi, also tawny

above instead of dark brown, and brighter orange-rufous below. Juvenile spotted above, streaks below more obscure. **VOICE.** Territorial call deep "who-who"; also cat-like mewling.

Habitat. Deep, wooded ravines, stream banks and pools in heavy broadleaf forest near water; prefers running water. From plains to c. 1500 m; usually at 250-365 m in Nepal, locally to 1525 m; occasionally to 2450 m in India.

Food and Feeding. Diet mostly fish; also crayfish, crabs, rodents, lizards, large beetles; often kills large birds, including partridges, pheasants and junglefowl; remains of a porcupine (*Hystrix brachyura*) found at nest. Crepuscular and nocturnal; frequently diurnal, active even in bright daylight. Hunts from perch, swooping down to capture fish near surface of water.

Breeding. Lays Nov-Feb in W of range. Nest in old nest of raptor high in tree, or in hollow in ravine or river bank. 2 eggs, sometimes 1. No other information.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Currently considered Near-threatened. In W, very rare and local to uncommon; status elsewhere very poorly known, possibly not uncommon locally. Very few observations, however, and probably rare over most of its range. Forest destruction a likely threat.

Bibliography. Ali & Ripley (1981), Ali *et al.* (1996), Choudhury (1998), Delacour & Jabouille (1940), Duckworth *et al.* (1998), Échécopar & Hue (1978), Grimmett *et al.* (1998), Inskipp & Inskipp (1991), Majumdar *et al.* (1992), Ripley (1982), Smythies (1986), Stepanyan (1995), Sun Yuanhsun & Wang Ying (1997), Sun Yuanhsun *et al.* (1997), Thewlis *et al.* (1998), Thompson *et al.* (1993), Tymstra *et al.* (1997), Voous (1988), Wang Sung (1998), Zhao Zhengjie (1995).

89. Buffy Fish-owl

Ketupa ketupu

French: Kétoupa malais **German:** Sundafischuhu **Spanish:** Búho Pescador Malayo
Other common names: Javan/Malay/Malaysian Fish-owl

Taxonomy. *Strix Ketupa* Horsfield, 1821, Java.

Genus *Ketupa* sometimes merged with *Bubo*, or treated as a subgenus; separated on basis of slight differences in skull morphology. Probably forms superspecies with *K. flavipes*, the two replacing each other geographically. Race *minor* sometimes incorrectly referred to as "*buetikoferi*". Race *aagaardi* intergrades with nominate *ketupu*. Four subspecies recognized.

Subspecies and Distribution.

K. k. aagaardi (Neumann, 1935) - S Assam to S Thailand and Vietnam.

K. k. ketupu (Horsfield, 1821) - Malay Peninsula, Riau Archipelago, Sumatra, Bangka, Belitung, Java, Bali, and Borneo (except NW).

K. k. minor Büttikofer, 1896 - Nias I, off W Sumatra.

K. k. pageli (Neumann, 1935) - NW Borneo.

Descriptive notes. 38-44 cm. Smallest fish-owl. Facial disc pale buff, with white eye-brows; upperparts buff, streaked with dark brown, feathers edged with pale rufous; scapulars whitish or pale buff; flight-feathers barred dark brown and buff; tail dark brown with 2-4 whitish bars; warm buff below, streaked with dark brown, streaks becoming thinner and sparser on belly and flanks; tarsi unfeathered; talons long and curved; iris bright, pale yellow; bill blackish; feet pale yellow-grey to greenish-yellow. Differs from *K. zeylonensis* in deeper, warmer buff colour below, lacks thin wavy bars on underparts. Juvenile more russet and less white-spotted above, tail with 5-6 whitish bars. Race *aagaardi* paler than nominate; *pageli* strongly tinged red; *minor* small. Voice. Loud "kootookookootook...", ringing "pof pof pof", and musical "to-who-to-who"; also hisses, mews and shrieks.

Habitat. Forest bordering streams, rivers, and lakes; also trees beside rice fields and fish ponds, old plantations, parks and large gardens near wetlands, and mangroves; often close to habitations. Mainly in lowlands and plains, locally up to 1100 m; to over 1600 m in Sumatra.

Food and Feeding. Mostly fish; also frogs, crustaceans, reptiles, large aquatic insects, small mammals (rats, mice) and birds; once a tortoise; also carrion, e.g. crocodile and badger. Forages at night, but frequently emerges from roost in late afternoon. Hunts from perch, swooping to catch fish from water surface; also stands beside or in shallow water to catch prey, and actively searches by walking in water.

Breeding. Lays Dec-May, mainly Jan-Apr; Jul-Apr in Malay Peninsula. Nest in cavity of large tree, or in tree fork, or in old raptor nest, occasionally on rock ledge; frequently among fronds of bird's-nest fern (*Asplenium nidus*). 1 egg, rarely 2 (only 1 chick survives); incubation 28-29 days; fledging c. 45 days.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Status poorly known; uncommon in Thailand; locally uncommon to more or less common in Malay Peninsula and SE Asia; common in Borneo. No recent records from Assam, where presumably rare or extinct. Seems to be fairly adaptable, able to occupy reasonably wide range of wooded and watery habitats. Some persecution locally, mainly in areas with fish ponds.

Bibliography. Andrew (1992), Bucknill & Chasen (1990), Delacour (1947), Delacour & Jabouille (1940), Duckworth & Kelsch (1988), Eates (1939), Glenister (1951), Grimmett *et al.* (1998), Hellebrekers & Hoogerwerf (1967), Higgins (1999), Hoogerwerf (1949a), Horne (1996a, 1996b), Lekagul & Round (1991), Lim Kim Seng (1992), MacKinnon (1988), MacKinnon & Philipps (1993), Madoc (1976), van Marle & Voous (1988), Medway & Wells (1976), Meyer de Schauensee & Ripley (1940), Nazimuddin (1993), Riley (1938), Ripley (1982), Rutgers & Norris (1972), Smythies (1981, 1986), Stepanyan (1995), Wells (1999).

Genus *NYCTEA* Stephens, 1826

90. Snowy Owl

Nyctea scandiaca

French: Hârfang des neiges **German:** Schnee-Eule **Spanish:** Búho Nival
Other common names: Snow Owl

Taxonomy. *Strix scandiaca* Linnaeus, 1758, Lapland.

Affinities uncertain. Probably closest to *Bubo*, but generically distinct on basis of skull characters and DNA. Monotypic.

Distribution. Breeds from W & N Scandinavia E across N Russia and N Siberia, including Novaya Zemlya, to Chukotskiy Peninsula. Anadyrland, N Koryakland and Commander Is; then North America in W Aleutians (Attu and Buldir), Hall I in Bering Sea, and from W Alaska E through N Canada to

N Labrador, including Banks, Prince Patrick and N Ellesmere Is; also N Greenland. Has bred occasionally in Iceland and N Britain (Shetland Is).



Descriptive notes. Male 55-64 cm, 700-2500 g; female 60-70 cm, 780-2950 g. Large white owl with small eyes, rudimentary ear-tufts normally invisible. Male entirely white, or with narrow, sparse, pale grey or brown barring on back, wings and/or tail; tarsus and toes with thick white feathering; iris brilliant golden-yellow, at times almost orange, eyelids blackish-edged; bill horn-black, nearly concealed by feathering; claws horn-coloured to black. Female noticeably bigger, crown spotted dark, moderate to extensive barring above and below, wings and tail more prominently barred blackish, but variable, sometimes almost male-like. Juvenile dark mouse-brown, feathers tipped and speckled greyish-white, barred; immature male like adult female, immature female even more heavily barred. Voice. When disturbed, a repeated "kre" call, uttered in flight; female may produce a loud, intense whistling or mewing note, during such situations as coition; when excited, male may utter low, rapid, and repeated cackling "ka"; female produces a higher pitched but similar "ke" note; also, male makes a loud, booming "hoo, hoo," usually double, but sometimes numbering six or more, the last often the loudest, and 1-2 second intervals after each. Male song a loud, booming "goo, goo", usually 2 notes but sometimes up to 6 or more, the last often loudest; female higher-pitched, notes often disyllabic; alarm a rapid, repeated cackling "kre-kre-kre..."; female also produces loud, intense whistling or mewing notes.

Habitat. Open tundra from near tree-line to edge of polar seas, with hummocks, rocks or other low prominences, and sparse low vegetation and dwarf shrubs and lichen; locally also coastal fields and open moorland, and will also use lowland salt meadows and poorly drained freshwater meadows; in general, breeds in areas with plentiful supply of arctic or subarctic rodents, usually at elevations below 300 m, except in Norway (where lemmings occur only on mountains at 1000 m or higher). In winter, also marshes, fields and dunes.

Food and Feeding. Lemmings (*Lemmus*, *Dicrostonyx*) and other voles (*Microtus*, *Clethrionomys*) major food items, at times probably exploited exclusively; other prey taken according to availability, include other mammals to size of hares, birds to size of ptarmigans (*Lagopus*), ducks and medium-sized geese, occasionally fish, amphibians, crustaceans and beetles. In Fennoscandia, of 2700 identified prey items, about a third were lemmings, and most (50-6%) were voles; in Shetland Is, where lemmings and voles absent, fed on rabbits or, when those rare, on chicks of various wading birds. In non-breeding season, mainly small mammals and birds, and some carrion; in British Columbia, grebes (mostly *Podiceps*) and ducks comprised 80% of prey by weight; in NE USA, where mammals abundant, rats and mice 35%, snowshoe hares 20%, and passerine birds 10% of diet. Most active at dusk and dawn, but forages throughout day in summer; on Baffin I, hunts in all weathers and at all hours during continuous summer light, seemingly less around noon and midnight; details of activity during winter darkness uncertain. Hunts from perch, making low, often long flight to capture prey on ground; acute vision and hearing enables it to locate lemmings beneath snow; takes birds also from water's surface, or pursues them in air; sometimes hovers; also pounces while standing or walking; said to catch fish while lying lengthwise belly down on rock by water hole. Small prey eaten whole, head first; larger ones first torn into pieces; birds sometimes partly plucked.

Breeding. Season May-Sept. Monogamous, often pairs for life; occasional polygyny and polyandry. Nest a shallow scrape on ground, usually in slightly elevated site (e.g. hummock, boulder) providing good view; territory c. 3-4 km² but highly variable according to food abundance, can be much larger when prey scarce. Undulating courtship flight by male a series of flaps followed by glide with wings held in dihedral. Clutch size varies with food supply, 3-5 eggs when limited, 7-11 when plentiful, average in Finnish Lapland 7-74; eggs laid at 2-day intervals; incubation 31-33 days, by female, fed on nest by male; chick with greyish-white down; young brooded and fed by female, male delivers food to nest; young can walk outside nest at 14 days, most remain a few days longer, leave at 20-28 days still unable to fly; first attempts at flight at age of c. 35 days, fly well after 50 days, cared for by parents for at least further 10 weeks. Success very variable, even among neighbouring pairs; in Canada, 1 nest produced 11 young from 11 eggs, another 4 young from 10 eggs; in ideal conditions can be very high, e.g. 31 fledglings from 32 eggs in Canada; success dependent on food supply and timing of spring thaw, nesting aborted where food scarce; main causes of nestling mortality starvation, and chilling. First breeding probably at 2 years. Longevity 10 years or more in wild; captive bird lived at least 28 years.

Movements. Mostly migratory and nomadic; some remain in breeding area all year if conditions allow. Movements not predictable, related in ways not fully understood to abundance of prey species; thought to vary considerably from region to region across polar tundra, and intensity of movements fluctuates annually; Nearctic populations periodically irruptive, many or most leaving breeding areas when lemming numbers crash. Winters irregularly S to C & SC USA, N & C Europe, NC Russia, NW & NE China and Japan, occasionally farther S; on average, immature males winter farthest S, adult females farthest N, with adult males and immature females in between. Vagrants recorded as far S as Bermuda and Azores.

Status and Conservation. Not globally threatened. CITES II. Generally uncommon to scarce. In North America, overall status presumed little changed; however, unpredictability of species' prey-dependent breeding densities and wintering distribution make such statements of doubtful value and impossible to test. Many apparently die from starvation during movement S from arctic regions; in examination of specimens in Alberta, however, 45% had moderate to heavy fat deposits, and only 14-1% believed to have starved; in that study, traumatic injuries were major cause of mortality, including collisions with unknown objects (46-5%), automobiles (14-1%), utility lines (4-2%) and airplanes (1-4%), also gunshot wounds (12-7%), electrocution (5-6%), and entanglement in fishing tackle (1-4%). In N Europe believed to have declined, but no real information on any long-term trends; rarity may be due to humans as much as to contraction of arctic habitats; in N Scandinavia, breeding density 40-55 pairs/100 km² in one peak lemming year, but only 15 pairs/100 km² in next peak year; species no longer breeds in Shetland and rarely does in Iceland. No information on N Asian populations. Protective measures prohibit the shooting and trapping of owls for any reason; harvesting of species for food, feathers and claws by native peoples may have local impact on population, but unlikely to have any wider effect on total numbers; policies enacted to protect large birds from electrocution and airplane strikes should benefit this species.

Bibliography. Ali & Ripley (1981), Andersson & Persson (1971), Armstrong (1983), Baieich & Harrison (1997), Beaman & Madge (1998), Blom (1998), Boxall & Lein (1982a, 1982b, 1982c, 1983, 1989), Brazil (1991), Brazil & Yamamoto (1989a), Breen-Smith & James (1995), Busse & Busse (1976), Campbell & MacColl (1978), Campbell *et al.* (1990), Chamberlin (1980), Cramp (1985), Custer (1973), Dancy (1983), Dorogin (1990, 1991), Duffy *et al.* (1976), Eckert, A. W. (1974), Eckert, K. R. (1997), Échécopar & Hue (1978), Evans (1980), Flint *et al.* (1984), Forsman (1998), Fragner (1995c), Fujimaki (1987), Gessaman (1968, 1972, 1978), Hagemeijer & Blair (1997), Hagen (1960),

Hakala *et al.* (1974), Hanson (1971), Heintzelman (1992), Húe & Échécopar (1970), James, R.D. (1980), Johnsgard (1988), Josephson (1980), Kaufman (1996), Kennedy *et al.* (1982), Kerlinger & Lein (1986, 1988a, 1988b), Kerlinger (1985), Knystautas (1993), Korpimäki (1992a), Lein & Boxall (1979), Lein & Webber (1979), Lindberg (1994a), Litvin & Ovsyanikov (1990), Marquis *et al.* (1989), Martin, B.P. (1992), Mikkola (1983), Miller (1987), Miller *et al.* (1975), Ovsyanikov & Menushina (1986), Parker (1974), Parmelee (1992), Portenko (1973), Robinson & Becker (1986), Rogacheva (1992), Root (1988), Rutgers & Norris (1972), Scherzinger (1974c, 1974d), Siegfried *et al.* (1975), Simeonov *et al.* (1990), Small (1994), Smith & Ellis (1989), Smith, N. (1994), Snow & Perrins (1998), Solheim (1989), Stefanzi (1983), Stepanyan (1990), Taylor (1973, 1974), Tremblay *et al.* (1998), Tyler & Phillips (1978), Voous (1988), Walker (1993), Watson (1957), Wiklund & Stigh (1983, 1986), Williams & Frank (1979), Windels (1981), Wolfe & de la Torre (1990), Young (1973), Zhao Zhengjie (1995).

Genus SCOTOPELIA Bonaparte, 1850

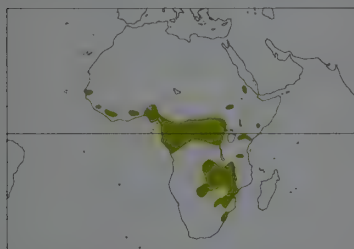
91. Pel's Fishing-owl

Scotopelia peli

French: Chouette-pêcheuse de Pel **German:** Bindenfischeule **Spanish:** Cárabo Pescador Común
Other common names: African Fishing-owl/Fish-owl

Taxonomy. *Strix peli* Bonaparte, 1850, Ashanti, Ghana. Relationships of genus uncertain. Monotypic.

Distribution. Locally from Senegambia E to Benin, and from Nigeria S across Congo Basin and C Africa to Botswana, Mozambique and NE South Africa; also SE Sudan, Ethiopia, S Somalia, Kenya and Tanzania; status in S Mali, Burkina Faso and S Niger unclear.



Descriptive notes. c. 55-63 cm; wingspan c. 150 cm; female 2055-2325 g. Largest fishing-owl. Round head with long "loose" feathering, no ear-tufts, lacks prominent facial disc; rufous upperparts with fine dusky bars, scapulars with some buff-white, tail with broad dusky bars; paler rufous below, with fine dusky streaks, becoming chevron marks on flanks; tarsus and toes unfeathered; iris dark brown; bill dark grey. Considerable individual variation in colour and barring, some with albinistic or melanistic feathers. Sexes similar, female often paler than male. Juvenile with body and head whitish, washed rufous; as adult at 15 months. VOICE.

Male gives sonorous hoot, usually followed by deep grunt, "hoooommm-hut", audible to 3 km; female may respond with higher hoot followed by double note "hoot-oot".

Habitat. Forested edges of lowland rivers, swamps and lakes, and estuaries; favours large riparian trees with deep cover and shade, also river islands. Sea-level to 1700 m.

Food and Feeding. Mainly fish; also some frogs, crabs and freshwater mussels; occasional large insects. Most fish prey in size range 100-200 g, but up to 2000 g recorded. Normally nocturnal; occasionally emerges during day. Hunts from perch 1-2 m above water, usually shallow, gliding down to snatch prey from surface, rarely submerging partially; sometimes wades into water from bank. Prey probably detected visually, from surface ripples; acoustical cues probably not used (transmission of sound across water-air interface poor), but squeakers, a major item of diet, produce sound by grating their fin bones, may reveal their general location.

Breeding. Lays Oct-Jun, peak Feb-Apr; timed to ensure brood-feeding at period when water level falling and prey concentrated. Monogamous. Nest 3-12 m up in natural cavity in tree, within 200 m of water; territory often quite small. 1-2 eggs, usually only 1 chick surviving; incubation c. 32-33 days, by female, fed by male; chick with white down, brooded and fed by female, food caught by mate; fledges at 68-70 days, remains within parental territory 6-9 months after fledging. In Botswana, 13 pairs made 10 breeding attempts, fledged 5 chicks; 4 of 13 eggs added, eggs and chicks disappeared for unknown reasons; when successful, may not breed in following year.

Movements. Resident; seasonal fluctuations in water levels force some to move to adjacent territories or floodplains.

Status and Conservation. Not globally threatened. CITES II. Common in Congo Basin, in Botswana (Okavango delta), and in swamps of Caprivi Strip in NE Namibia and also those in C Africa; also common locally in Transvaal, e.g. along R Levubu. Appears to be uncommon to rare in rest of range: e.g. in Kenya, known only from R Tana and secluded parts of R Mara; rare and local in W Africa. Overall densities variable. 1 pair/1-10 km of river, depending on number of suitable sites for fishing, nesting and roosting. Variable conditions, with cycles of drought, severely disrupt its normal lifestyle; sometimes forced to forgo breeding, and immatures may have trouble finding suitable stretch of river on which to establish territory; many starve during dry season. Destruction of riverine growth a threat. Damming and silting of rivers can have adverse effect on species, and in some areas water pollution possibly a problem. Further study needed.

Bibliography. Ash & Miskell (1998), Atkinson, Koroma *et al.* (1994), Bannerman (1953), Barlow *et al.* (1997), Benson & Benson (1977), Benson *et al.* (1971), Brooke (1984), Brown (1976, 1977), Campbell (1977), Cheke & Walsh (1996), Claffey (1997), Davey (1978), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Elgodd *et al.* (1994), Fabian (1988), Field (1998), Fry *et al.* (1988), Gatter (1997), Ginn *et al.* (1989), Giraudoux *et al.* (1988), Gore (1990), Grimes (1987), Harrison *et al.* (1997), Hickman & Berry (1998), Ives (1991), Kemp & Calburn (1987), Kemp & Kemp (1998), Lewis & Pomeroy (1989), Liversedge (1980, 1981, 1982), Mackworth-Praed & Grant (1957, 1962, 1970), Maclean (1993), Penny (1994), Pickford *et al.* (1989), Pinto (1983), Riddell (1987), Sereech (1999), Short *et al.* (1990), Snow (1978), Steyn (1982, 1984, 1988, 1994c), Thompson (1972), Wilkinson (1999), Woolley (1980), Zimmerman, D.A. *et al.* (1996).

92. Rufous Fishing-owl

Scotopelia ussheri

French: Chouette-pêcheuse rousse **Spanish:** Cárabo Pescador Rojizo
German: Rotrückten-Fischeule

Taxonomy. *Scotopelia ussheri* Sharpe 1871, Fantee, Ghana.

Relationships of genus uncertain. Monotypic.

Distribution. Sierra Leone, Liberia, Ivory Coast and Ghana; possibly also Guinea.



Descriptive notes. 46-51 cm; 1 male 743 g. Head tawny, with no distinct facial disc or ear-tufts; dark rufous above, scapulars with some buff-white; flight-feathers and tail tawny-rufous with narrow dark bars; face and underparts light cinnamon, breast with narrow rufous streaks; tarsus and toes unfeathered; iris dark brown (sometimes erroneously stated to be yellow); bill black; legs and feet light yellowish. Differs from *S. peli* in smaller size, unbarred upperparts, lack of chevron pattern below. Juvenile with light buffy-white body and head; probably gains adult plumage c. 6 months after fledging. VOICE. Deep, dove-like

"ooo", repeated at 1-minute intervals.

Habitat. River and lagoon edges in lowland forest, mainly primary but also secondary forest and degraded habitat, and sometimes plantations; also recorded in coastal mangroves.

Food and Feeding. Little known; catfish found in 1 stomach. Hunts at night, occasionally in afternoon; observed on perch above a stream in high, dark forest, also resting on sandbar.

Breeding. Very little known. Nestlings collected in Sierra Leone suggest only 1 young raised from egg laid Sept-Oct; in Liberia, juvenile still with downy plumage in Mar, immature with mostly adult plumage in Jul. Biology probably similar to that of *S. peli*.

Movements. Probably resident; possibly some local movements, as with *S. peli*.

Status and Conservation. ENDANGERED. CITES II. Restricted-range species; present in Upper Guinea Forests EBA. Population unknown; only 17-20 records during 1870-1983. Reported as fairly common in Sierra Leone (Loma Mts) in 1992; thought not uncommon in Liberia in 1990's; very few records from Ivory Coast (perhaps owing to confusion over voice); only c. 5 records from Ghana; and single record from Guinea. Small number of observations suggests that species is rare, although it may be overlooked because of its elusive nature. Main threats are clearance of mangrove and forest, and river pollution; iron-ore mining has caused severe pollution to R Mano between Sierra Leone and Liberia, and R Yah in Liberia; in addition, young are captured and kept as pets by local inhabitants. Occurs in a few protected areas through its range, including Gola Forest Reserve (Sierra Leone), Sapo National Park (Liberia) and Tai Forest National Park (Ivory Coast). Survey and monitoring of existing population required.

Bibliography. Allport (1991), Allport *et al.* (1989), Atkinson, Koroma *et al.* (1994), Bannerman (1953), Barlow (1998), Bouet (1961), Clark & Mikkola (1989), Collar & Andrew (1988), Collar & Stuart (1985), Collar *et al.* (1994), Colston & Curry-Lindahl (1986), Demey & Fishpool (1991), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Dutton & Branscombe (1990), Field (1998), Fishpool (1994), Fishpool *et al.* (1989), Fry *et al.* (1988), Gartshore (1989), Gartshore *et al.* (1995), Gatter (1988, 1997), Grimes (1987), Hald-Mortensen (1971), Kemp & Kemp (1998), Louette (1974), Mackworth-Praed & Grant (1970), Rand (1951b), Schouteden (1970), Snow (1978), Stattersfield *et al.* (1998), Thiollay (1985), Turk (1998), Wilkinson (1999).

93. Vermiculated Fishing-owl

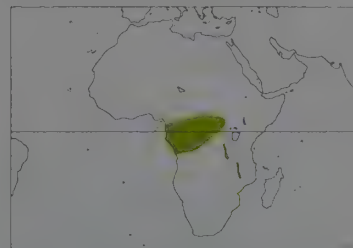
Scotopelia bouvieri

French: Chouette-pêcheuse de Bouvier **Spanish:** Cárabo Pescador Vermiculado
German: Marmorfischeule

Taxonomy. *Scotopelia bouvieri* Sharpe, 1875, Lopé, Ogowe River, Gabon.

Relationships of genus uncertain. Monotypic.

Distribution. Congo Basin in S Cameroon, Gabon, Central African Republic, Congo, Zaire, and extreme NW Angola; possibly SE Nigeria.



Descriptive notes. 46-51 cm. Head buffy-rufous with black streaks on forehead, no ear-tufts, inconspicuous light rufous facial disc; upperparts dark rufous-cinnamon with fine dark brown vermiculations, scapulars with variable whitish on outer webs; flight-feathers and tail rufous with dark bars; underparts variably creamy to light rufous, with heavy dark brown streaks, undertail unmarked whitish; tarsi and toes unfeathered; iris dark brown; bill pale yellow. Juvenile cinnamon-washed white on body and head, streaked above, finer streaking below, flight-feathers more rufous. VOICE. Croaking hoot followed

by shorter, faster notes, "drook krook ook-ook ook-ook"; duets.

Habitat. Gallery forest fringing large rivers, within primary forest; prefers rivers 10 m or more in width; also smaller rivers, and pools in swamp-forest or temporarily flooded forest; occasionally away from water.

Food and Feeding. Small fish, frogs, crustaceans, fiddler crabs, and small birds and mammals; appears to eat more crabs and crustaceans than other fishing-owls. Nocturnal. Hunts from perch 1-2 m above water.

Breeding. Lays May-Oct; in Zaire probably as late as Nov-Dec. Uses old stick nest of large bird; recorded laying in nest of Spot-breasted Ibis (*Lamprolaima rara*). 1-2 eggs, 1 nestling surviving; incubation and fledging periods unrecorded. Longevity over 27 years in captivity.

Movements. Probably resident; may make similar movements to *S. peli* during periods of drought. **Status and Conservation.** Not globally threatened. CITES II. Little is known about its biology; this may be because of its secretive lifestyle and remote habitat preferences or because it exists in small numbers. However, may be relatively common on large rivers in the Congo Basin. Further study is necessary to quantify its status.

Bibliography. Atkinson, Koroma *et al.* (1994), Bannerman (1953), Brosset & Énard (1986), Busse (1989), Dowsett & Dowsett-Lemaire (1991, 1993), Dowsett & Forbes-Watson (1993), Dowsett-Lemaire (1996), Elgodd *et al.* (1994), Fry *et al.* (1988), Gatter (1988), Kemp & Kemp (1998), Lippens & Wille (1976), Mackworth-Praed & Grant (1970), Pinto (1983), Sargeant (1994b), Snow (1978), Wilkinson (1999).



Tribe STRIGINI

Genus *STRIX* Linnaeus, 1758

94. Spotted Wood-owl

Strix seloputo

French: Chouette des pagodes **German:** Pagodenkauz **Spanish:** Cárabo de las Pagodas
Other common names: Seloputo Owl

Taxonomy. *Strix Selo-puto* Horsfield, 1821, Java.

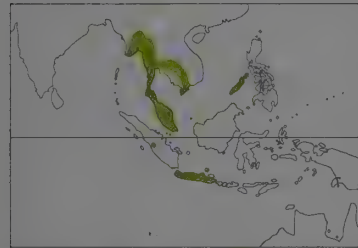
In the past, names *Strix orientalis* and *Strix pagodorum* have been used for this species, but both considered invalid. Race *wiepeni* previously referred to by the synonym *Surnia whiteheadi*. Three subspecies recognized.

Subspecies and Distribution.

S. s. seloputo Horsfield, 1821 - S Myanmar and C Thailand S to Sumatra (Jambi) and Java.

S. s. baweana Oberholser, 1917 - Bawean I, off N Java.

S. s. wiepeni (Blasius, 1888) - Calamian Is and Palawan, in W Philippines.



Descriptive notes. 45-47 cm; male 1011 g. Rusty facial disc; upperparts dark brown, head and upper neck almost black, lower back russet, entire dorsal surface covered with black-edged white spots, which extend to forecrown; white barring on upperwing-coverts; scapulars white, striped with dark brown; chin buff-colored; throat white with brown edging, sides of neck barred with white; remaining ventral surface white, tinged russet on breast, all barred dark; tarsus feathered white with dark bars; iris dark brown; bill greenish-black; toes grey. Differs from *S. leptogrammica* in much bolder, broader dark brown barring below. Juvenile

prominently barred; immature often with much white above. Race *baweana* smaller, paler, with narrower bars below; *wiepeni* with yellowish-rufous ground colour below. Voice. Deep and forceful "who", usually preceded by rolling "huhuhuhuh", repeated; also described as resonant, rising "beloop" or "hoop-hoong"; deep growling call also reported.

Habitat. Lowland open forest and forest edge, stands of trees near habitation, orchards, suburban and urban parks, and paddyfields; also noted in mangrove forest and open deforested areas. Sea-level to c. 1000 m, mostly below 800 m.

Food and Feeding. Mostly small rodents, small birds and large insects; often takes Tree Sparrows (*Passer montanus*). Still-hunts from perch 2-3 m above ground.

Breeding. Probably Jan-Jun in Malay Peninsula; young fledglings noted in Mar, Apr, Jun and Aug. Nest in tree cavity, 2-18 m up; sometimes on top of bird's-nest fern (*Asplenium nidus*). 2 eggs, occasionally 3.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Reports vary; apparently common in Myanmar; uncommon in Thailand, but said to be more or less common in Peninsular Malaysia, e.g. in Pasoh Forest Reserve; scarce in Java, and only a couple of records from Sumatra. Possibly overlooked as a result of its rather secretive habits, although species seems to occur at naturally low densities.

Bibliography. Andrew (1992), van Balen (1968), Hellebrekers & Hoogerwerf (1967), Holmes (1996), Hoogerwerf (1949a), Lekagul & Round (1991), Lim Kim Seng (1992), MacKinnon (1988), MacKinnon & Philipps (1993), Manuel (1939), van Marle & Voous (1988), McGregor (1909-1910), Medway & Wells (1976), Riley (1938), Smythies (1986), Wells, D.R. (1990, 1999).

95. Mottled Wood-owl

Strix ocellata

French: Chouette ocellée **German:** Mangokauz **Spanish:** Cárabo Ocelado

Taxonomy. *Syrnium ocellatum* Lesson, 1839, Pondicherry.

Race *griseocens* intergrades with nominate *ocellata* in N India. Three subspecies recognized.

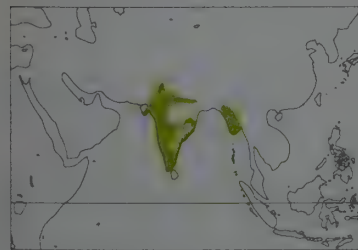
Subspecies and Distribution.

S. o. griseocens Koelz, 1950 - from base of Himalayas in Pakistan S to about Rajasthan, and E to Bihar.

S. o. grandis Koelz, 1950 - S Gujarat (Saurashtra Peninsula).

S. o. ocellata (Lesson, 1839) - peninsular India.

Apparently resident also in W Myanmar, but race undetermined.



Descriptive notes. 40-48 cm. Facial disc white with concentric black barring, and some rufous-orange mottling; upperparts grey, mottled and vermiculated with reddish-brown, black, white and buff; flight-feathers and tail barred grey-brown and black; throat chestnut and black with white stippling; prominent white collar on neck side; underparts white to golden with narrow blackish cross-bars; tarsus feathered buffish; iris brown; bill horn-black. Juvenile undescribed. Races differentiated primarily on basis of wing length and tone of upperparts: *grandis* and *griseocens* larger than nominate, *grandis* greyer above, *griseocens* paler above. Voice. Main

breeding-season vocalization described as quavering "chuhua-aa"; during other seasons calls consist of single metallic hoot and an occasional screech.

Habitat. Wooded plains, clumps of mango trees, tamarind and banyan groves, densely foliated trees on outskirts of villages and cultivation; confined to lowlands.

Food and Feeding. Rats, mice and other rodents, and small birds up to size of Rock Dove (*Columba livia*); also crabs, lizards, and large insects such as beetles; record of scorpion found in stomach.

Breeding. Lays Nov-Apr, Feb-Mar in N. Nest usually in natural, mostly unlined tree hollow, possibly rarely in old stick nest of other bird. Usually 2 eggs, occasionally 3; no other information.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Uncommon in India; no recent records from Pakistan, where extremely rare or possibly even extinct. Status in Myanmar uncertain; said to have been common in SW (Arakan) before 1950's, but no information since then.

Bibliography. Ali (1996), Ali & Ripley (1981), Baker (1934a), Daniels (1997), Grimmett *et al.* (1998), Mahabal & Lamba (1987), Mukherjee (1995), Perumal (1985a, 1985b), Ripley (1982), Roberts (1991), Smythies (1986).

96. Brown Wood-owl

Strix leptogrammica

French: Chouette leptogramme **German:** Malaienkauz **Spanish:** Cárabo Oriental
Other common names: Himalayan Brown Owl/Wood-owl ("*newarensis* group"); Bartels's Wood-owl (*bartelsi*); Malaysian Wood-owl (*maingayi*)

Taxonomy. *Strix leptogrammica* Temminck, 1831, Borneo.

Probably a species complex rather than a single species. N forms living in montane habitats (*newarensis*, *ticehursti*, *laotiana*, *caligata*) larger, with different vocalizations, likely to represent a separate, polytypic species. Race *bartelsi* likewise vocally distinct and living at higher elevations, probably also specifically distinct. In addition, Sri Lankan *ochrogenys* sometimes considered synonymous with *indranei*; *chuseni* possibly synonymous with nominate; *myrtha* and *nyctiphasma* doubtfully distinct from *maingayi*. Additional races described are *connectens* (single specimen from C India), included in *indranei*, and *orientalis* and *shahensis*, both treated as synonyms of *ticehursti*. Fourteen subspecies recognized.

Subspecies and Distribution.

S. l. newarensis (Hodgson, 1836) - Himalayas, from Jammu and Kashmir E to NE India.

S. l. ticehursti Delacour, 1930 - N & C Myanmar E to SE China (NE to Anhui), S to N & W Thailand, N Laos and N Vietnam.

S. l. caligata (Swinhoe, 1863) - Hainan and Taiwan.

S. l. laotiana Delacour, 1926 - S Laos and C Vietnam (Annam).

S. l. indranei Sykes, 1832 - peninsular India.

S. l. ochrogenys (Hume, 1873) - Sri Lanka.

S. l. maingayi (Hume, 1878) - S Myanmar, S Thailand and Malay Peninsula.

S. l. myrtha (Bonaparte, 1850) - Sumatra; also reported from Mentawai Is (possibly this race).

S. l. nyctiphasma Oberholser, 1924 - Banyak Is, off W Sumatra.

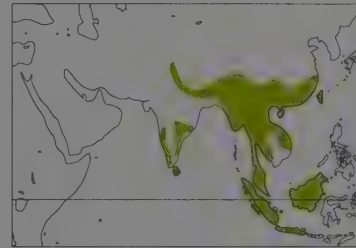
S. l. niasensis (Salvadori, 1887) - Nias I, off W Sumatra.

S. l. chuseni Hoogerwerf & de Boer, 1947 - Belitung I, off SE Sumatra.

S. l. vaga Mayr, 1938 - N Borneo.

S. l. leptogrammica Temminck, 1831 - C & S Borneo.

S. l. bartelsi (Finsch, 1906) - Java.



Descriptive notes. 40-55 cm; 500-700 g (*bartelsi*). Whitish to light rufous-brown facial disc with broad black ring around eyes; whitish eyebrows, occasionally with rufous tint; crown dark brown; upperparts lighter chestnut-brown, with some white or pale barring on scapulars and on wings and tail; chin dark brown; throat and underparts white to buffy, breast often brown, all with thin, indistinct brown barring; tarsus fully feathered; iris dark brown; bill greenish-horn. Juvenile light rufous, barred rusty, wings darker with dark rufous bars, underparts pale buff with faint bars. Races vary in size, depth of coloration, and

markings: *indranei*, *ochrogenys* and *maingayi* richer and darker brown, with dark rufous facial disc, more chestnut in *ochrogenys*; *vaga* slightly bigger than nominate, and duller, greyer; *niasensis* smaller, chest bright chestnut; *bartelsi* with more tawny facial disc, dark brown above, pale chin; "*newarensis* group" much larger, facial disc whitish to pale fulvous-brown, large white throat patch, brown chest band. Voice. Brief series of 3-4 short hoots, first ones very soft, last one longer and louder; also deep, 4-syllable "goke-goke-ga-looo" with emphasis on final note; barking "wow wow" alarm call also noted. Race *bartelsi* a distinctive, loud, explosive, forceful, single "hooh", repeated at long intervals; "*newarensis* group" "lo" "to-hooh" not unlike Rock Dove (*Columba livia*).

Habitat. Forest, usually dense and undisturbed, generally avoiding areas of human habitation; in N Indian Subcontinent often evergreen and moist deciduous, generally at 750-2500 m, but also reported up to 4000 m; dense, broadleaved forest at 760-2700 m in Nepal; to 2750 m in China and Taiwan; plains to 1800 m in peninsular India, also densely wooded gardens in Sri Lanka; noted both in montane forest and in open country in Thailand; primary forest in lowlands in Borneo and Sumatra, where recorded at up to 1500 m; undisturbed mountain forest and forest edge in Java.

Food and Feeding. Small mammals, especially rodents but also some shrews, and Javan specimen contained remains of fruit bat (*Cynopterus*) in stomach; also small birds and reptiles, and large insects; some reports of fish being taken. Bird prey apparently more important in N of range, include not only smaller species such as doves and mynas but also some up to size of pheasants; preference for partridges (*Arborophila*, *Bambusicola*) evident.

Breeding. Lays Jan-Mar in S India and Sri Lanka; Feb-Apr in Himalayas. Nest in cavity of tree, sometimes with few feathers added; in Himalayas, also on rock ledge on cliff face, or in cave, or a scrape on ground, generally at base of tree or rock. 2 eggs, occasionally 1; incubation at 1 site 30 days.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Uncommon throughout most of range in Indian Subcontinent, and rare and local in Bangladesh; possibly more common, or locally com-

mon, in Sri Lanka; rare in Java, where ongoing clearance of mountain forest represents a major threat; in rest of range appears to be uncommon to rare, and again suffering from forest destruction. Occurs in several protected areas throughout its range, such as Chitwan National Park (Nepal), Nam Nao National Park and Khao Nor Chuchi Wildlife Sanctuary (Thailand), Way Kambas National Park (Sumatra), Gunung Mulu National Park (Sarawak), Danum Valley Conservation Area (Sabah), Barito Ulu National Park (Kalimantan) and Baluran National Park (Java).

Bibliography. Ali (1996), Ali & Ripley (1981), Ali *et al.* (1996), Deignan (1945), Delacour & Jabouille (1940), Échécopar & Hùe (1978), Grimmett *et al.* (1998), Holmes (1996), Inskipp & Inskipp (1991), Lekagul & Round (1991), MacKinnon & Philipps (1993), Majumdar *et al.* (1992), van Marle & Voous (1988), Medway & Wells (1976), Phillips (1978), Ripley (1938), Ripley (1977, 1982), Roberts (1991), Smythies (1981, 1986), Voous (1988), Wells (1999), Whymper (1906), Zhang Cizu *et al.* (1997), Zhao Zhengjie (1995).

97. Tawny Owl

Strix aluco

French: Chouette hulotte **German:** Waldkauz **Spanish:** Cárabo Común
Other common names: Eurasian Tawny Owl/Wood-owl, Tawny Wood-owl

Taxonomy. *Strix Aluco* Linnaeus, 1758, Sweden.

Probably forms superspecies with *S. butleri*; formerly considered to include latter as race. Geographical limits of races obscure; nominate *aluco* intergrades with *siberiae* and *sylvatica* with *sanctinicolai*. Several additional races named, but considered probably not acceptable because of species' considerable individual variation and polymorphism; populations from Iberia, Asia Minor and Middle East sometimes separated as *clanceyi*, those from SW Russia as *volhyniae*, and those from S Caspian as *obscurata*. Eleven subspecies recognized.

Subspecies and Distribution.

S. a. aluco Linnaeus, 1758 - N & E Europe E to W Russia (Ural Mts), S to Alps, Balkans and Black Sea; intergrades with .

S. a. siberiae Dementiev, 1933 - from Ural Mts to W Siberia.

S. a. sylvatica Shaw, 1809 - Britain, France and Iberia; probably this race also from S Italy and Greece E to W & C Turkey and Middle East; intergrades with *sanctinicolai*.

S. a. mauritanica (Wetherby, 1905) - NW Africa (Morocco to Tunisia).

S. a. willkenskii (Menzbier, 1896) - NE Turkey, Caucasus and NW Iran, E to Turkmeniya.

S. a. sanctinicolai (Zarudny, 1905) - NE Iraq and W Iran.

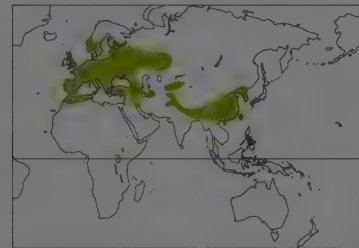
S. a. harmsi (Zarudny, 1911) - Turkistan.

S. a. biddulphi Scully, 1881 - Pakistan and NW India.

S. a. nivicola (Blyth, 1845) - Nepal E to SE China, S to N Myanmar and N Indochina.

S. a. ma (Clark, 1907) - NE China (Jilin) and Korea.

S. a. yamadae Yamashina, 1936 - Taiwan.



Descriptive notes. 37-39 cm; wingspan 94-104 cm; male average 440 g, female average 553 g (nominate *aluco*). Medium-sized owl with noticeably stocky body, large and round head; plumage polymorphic, with intermediates. Nominant race mostly grey-brown, facial disc generally pale with some darker concentric rings, crown with dark centre bordered by pale bands; upperparts heavily mottled brown with darker shaft streaks, outer webs of outer scapulars and upperwing-coverts with large white or cream spot at tip; underparts streaked dark and with variable thin cross-bars; tarsus and most of toes feathered; iris blackish-brown; bill horn-coloured to pale yellowish; toes grey. Morphs vary mostly in ground colour of plumage, from deep rufous-brown to dark grey: rufous morph rufous-chestnut to rufous-cinnamon above, facial disc deep rufous-cinnamon with contrasting white arcs from above each eye and from lower cheek joining at base of bill; intermediate birds have hindneck and crown buff to pale cream-yellow with broad black streaks, remainder of upperparts buff-brown to grey-brown with less distinct narrow dark bars and vermiculations, and facial disc off-white with grey concentric lines; grey morph pale buff to grey-buff above, sometimes mixed with white on crown and hindneck; dark grey morph has plumage dominated by narrow dense black bars on crown and hindneck, dense dark grey vermiculations on rest of upperparts, and pale grey facial disc with much dark grey barring and mottling. Juvenile paler, plumage noticeably looser, even shaggy, and more finely barred. Races differ in colour and size, but difficult to distinguish owing to large individual variation: *sylvatica* smallest, usually rufous-brown or tawny-chestnut; *mauritanica* larger, wingspan up to 20% greater than nominate and *sylvatica*, always grey-brown; *siberiae* distinctly paler, with much white; *nivicola* largest, longest-winged, more barred than streaked below. **VOICE.** Long, quavering hoot, followed by faint monosyllable, a short pause, and then extended soft tremolo which falls in pitch; during courtship also long trills; also soft "quii" calls probably as contact, and sharp "ke-wick" in excitement or aggression.

Habitat. Open and semi-open forest, woodland, farmland with trees, parks, larger gardens in villages and towns, and tree-lined urban avenues; also rocky areas with sufficient tree and bush cover; avoids large unbroken forest tracts, wetlands and treeless plains, as well as unduly windswept, frosty or arid climates; occurs from fringe of boreal zone through temperate regions and steppe to Mediterranean and related montane zones. For hunting, requires richly structured habitat with plenty of lookout posts, including sparse woodland, clearings, avenues, cemeteries, hedgerows and gardens, especially among mature trees, and with some preference for access to water. Mainly in lowlands, but ranges up to 2350 m in Turkey and to similar altitudes in Turkistan; even to 4250 m in Himalayas, where sometimes lives above tree-line.

Food and Feeding. Small mammals, from small rodents and shrews up to size of squirrels and young rabbits, and small birds up to size of pigeon; also amphibians, reptiles, earthworms, snails, beetles and other insects, occasionally fish; in urban areas, largely birds, small rodents and other prey taken as available; pellets often contain soil and plant remains, and sometimes composed of soft wood or sawdust. In pellet study in England, mice and voles found to constitute 56-4% of prey, and larger mammals 34-7% of diet; in Scotland, wood mouse (*Apodemus sylvaticus*) most commonly taken mammal prey and House Sparrow (*Passer domesticus*) most frequently identified bird prey. Diet shifts from mainly mammals in winter to primarily birds in breeding season, and from small prey to medium-sized (over 30 g) prey; in E Bohemia, fed mainly on *Microtus* voles, but in poor vole years switched to other food. Relative proportions of prey taken considered to reflect availability, rather than food specialization. Chiefly nocturnal, hunting between dusk and dawn; occasionally diurnal. Most prey located by sound. Hunts mostly from perch, turning body occasionally; makes frequent short flights, returning to same perch; glides or drops on to prey, extends

wings on impact to cover or strike prey; where habitat includes open ground, often flies slowly, with frequent intermittent glides, makes zig-zag searches, and hovers; reported to take fish from water surface while in flight, or by wading in shallows. Forages for earthworms by flying down to ground and waiting motionless until it appears to hear a sound, then rotating head and stretching neck, hopping forward, repeating head movements, and finally making 2-3 long leaps with wings partially spread to peck up worm. Bats and large insects also seized in flight. Usually consumes food on elevated perch.

Breeding. Season Feb-Jul; Jan-May in Himalayas. Monogamous, pairs for life; occasionally bigamous. Nest in hole in tree, also in cliff or building; often uses old nest of Magpie (*Pica pica*) or drey of squirrel (*Sciurus*); sometimes in hole in ground or among tree roots; readily accepts nestbox; fidelity to nest-site marked, although occasionally changes if site deteriorates or is disturbed; in Europe, average territory size from 10-12 ha in optimum habitat to 60-70 ha in poor habitat, and vocal responses to intruders found to be largely sex-specific. 2-9 eggs, usually 3-5, laying interval 2-4 days; female incubates and broods, fed by male; incubation 28-30 days; hatching asynchronous, chick with white down; young brooded until 15 days old; fratricide occurs when food short; fledging period 32-37 days, but will leave nest at 25-30 days and hide on nearby branches; independence 3 months after fledging. In Belgian study, of 256 eggs laid 24% did not hatch, of 195 young hatched 94% fledged, average brood size at fledging 2.06, varied depending on vole numbers; in Sweden, mortality in first year of life 71%, in second year 44%, in third year 48%; in Switzerland, mortality in first year 49%, in second and third years 25%. Age of first breeding 1-2 years. Oldest ringed bird 18 years 10 months.

Movements. Resident. Breeding adults remain in territory all year. Juveniles disperse by late autumn, in temperate areas usually within radius of a few km of natal site; in Fennoscandia, dispersal up to 20 km, but once 745 km into Lapland, and individuals disperse in all directions.

Status and Conservation. Not globally threatened. CITES II. Generally common throughout range. European population in mid 1990's estimated at c. 400,000-560,000 pairs, plus substantial numbers (up to 100,000 pairs) in W Russia and up to 20,000 pairs in Turkey; largest numbers in France and Germany, with c. 85,000 pairs in each, and c. 70,000 pairs in Poland and over 50,000 pairs in Spain; good numbers of pairs also in Croatia (20,000-25,000), Latvia (20,000), Sweden (15,000), Greece (15,000) and Belarus (10,000); British population estimated at around 20,000 pairs. Appears to be fairly stable or slightly increasing in C Europe, and possibly decreasing in N & S. In Britain, declined in 19th century through human persecution, but increased over much of that region from c. 1900 to 1930 (and in some areas to 1950), apparently stabilizing in mid 1970's at figure then put at 10,000-100,000 pairs (upper limit regarded as over-optimistic). Some expansion in range in Netherlands and Belgium, aided mainly by maturation of forest. Considered common in C parts of Russia, but less so in N, and scarce in Caucasus. Thought rather uncommon in China. In England, despite wide variations in numbers of prey and of fledged young produced, a studied population of adults remained notably stable; stability was maintained by those young which failed to find a territory either starving or moving outside area, which in most cases led to mortality; regulation of the population studied was thus due to territorial intolerance acting to produce subsequent mortality.

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98. Hume's Owl

Strix butleri

French: Chouette de Butler **German:** Fahlkauz **Spanish:** Cárabo Árabe
Other common names: Hume's Wood-owl/Tawny Owl, Desert Owl

Taxonomy. *Asio butleri* Hume, 1878, Omara, Makran Coast, southern Baluchistan.

Probably forms superspecies with *S. aluco*. Formerly treated as conspecific with latter, but clearly different in plumage, eye colour and vocal patterns, and ecology, as well as DNA. Monotypic.

Distribution. E & S Israel, Jordan, Sinai Peninsula and E Egypt (Red Sea mountains), and patchily in Arabian Peninsula (Saudi Arabia, Yemen and Oman); possibly still S Pakistan (Makran Coast), perhaps also S Iran.



Descriptive notes. 30-35 cm; wingspan 95-98 cm; c. 214-220 g. Resembles *S. aluco* in proportions and plumage pattern. White facial disc; crown with dark central band; upperparts light sandy-grey or greyish-yellow with dusky brown spots and streaks; distinct golden-buff collar across top of mantle, extending as wash across chest; scapulars and wing-coverts tipped pale buff or white; light and dark brown bars on flight-feathers and tail; underparts cream-coloured with some dark mottling or thin brown shaft streaks, lightly vermiculated on breast and flanks; tarsi feathered white; iris orange; bill yellowish-brown; toes greyish. Differs from *S. aluco* in smaller size, paler appearance, lack of heavy dark streaking, orange eyes.

Juvenile very pale, barred, with yellowish eyes. Voice. Long soft hoot followed by two shorter double hoots, "hoooo, hoo-u hoo-u", without tremulous character, repeated after a few seconds.

Habitat. Rocky gorges or canyons in semi-desert and desert, usually with water source nearby; also near acacias and palm groves, and sometimes at ruined buildings; occasionally near settlements.

Food and Feeding. Rodents such as gerbils (*Gerbillus*), jirds (*Meriones crassus*) and spiny mice (*Acomys russatus*); also lizards, birds (small passerines), scorpions, and grasshoppers and other insects. Nocturnal and crepuscular. Hunts mostly from perch, often near roads and tracks; also hawks insects in air; probably forages occasionally by walking on ground.

Breeding. Mar-Aug. Nest in cavity or cave in wall of steep gorge. Up to 5 eggs; incubation 34-39 days, by female, but confirmed record of both parents incubating; chick with white down; fledging period 30-40 days.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Israeli population tentatively estimated at 200 pairs in late 1980's; no numerical data from elsewhere. Originally thought to be fairly rare, this based primarily on fact that until middle part of 20th century almost all information on this species was gleaned solely from the type specimen, collected in Pakistan in 1878. Between 1950's and 1970's, more extensive studies carried out in Middle East, and as a result now considered relatively common in Israel. Fragmented distribution possibly misleading; terrain difficult to census. Not recorded in Pakistan since 1920, although region little visited by ornithologists. Main cause of mortality, at least in Israel, appears to be road traffic.

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99. Spotted Owl

Strix occidentalis

French: Chouette tachetée **German:** Fleckenkauz **Spanish:** Cábaro Californiano
Other common names: Mexican/Mountain Spotted Owl, Mountain Forest Owl (*lucida*)

Taxonomy. *Syrnium occidentale* Xántus de Vesey, 1860, Fort Tejon, California.

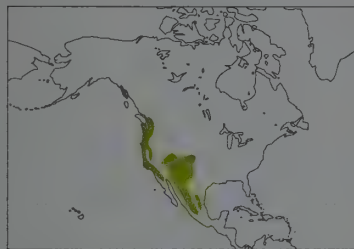
May be member of superspecies that includes *S. varia* and *S. fulvescens*. Occasionally hybridizes with *S. varia* in Mexico, where ranges overlap. Race *lucida* very pale, possibly specifically distinct. Three subspecies recognized.

Subspecies and Distribution.

S. o. caurina (Merriam, 1898) - SW Canada (British Columbia), S through W USA Coast Ranges to N California.

S. o. occidentalis (Xántus de Vesey, 1860) - C & S Californian Coast Ranges and W slope of Sierra Nevada, S to N Baja California.

S. o. lucida (Nelson, 1903) - from N Arizona, SE Utah and S Colorado S to N & C Mexico (S to Michoacán and Guanajuato).



Descriptive notes. 41-48 cm; male 520-700 g, female 550-760 g. Medium-sized brown owl; flight slow, quick wingbeats interspersed with gliding. Facial disc large, rounded, brownish, with indistinct concentric circles of darker brown around each eye; upperparts chocolate-brown to chestnut-brown with numerous round, elliptical or irregular white spots; remiges and rectrices dark brown, barred with light brown and white; underparts heavily barred brown and whitish; legs and feet fully feathered; iris almost black; bill yellowish-green. Differs from *S. varia* in smaller size, darker coloration, lack of vertical streaks on abdomen. Juvenile light

brown with dark transverse barring. Race *caurina* darker brown, with smaller white spots and markings; *lucida* lighter brown, with more white on facial disc and upper breast, more and larger white spots. VOICE. A 4-note "whoop hu-hu hoo", by both sexes, female somewhat higher and hoarser; also a hollow whistle, "cooo-weep", ending in upward inflection, mainly by female during breeding; rapid series of loud barking notes, "ow!-ow!-ow!-ow!-ow!", or single barks; apparently able to make fine adjustments to its own call to imitate that of neighbour.

Habitat. Mature coniferous and mixed forest, and wooded canyons; western hemlock (*Tsuga*), Douglas fir (*Pseudotsuga*), redwood (*Sequoia*), Douglas fir/hardwood, evergreen hardwood, pine-oak, ponderosa pine, western red cedar (*Thuja*) and other forest types, including riparian forest, as well as steep, rocky canyons in some parts of range. In one study, 98% of 636 occupied sites were in areas of old-growth forest, or mixtures of mature and old-growth timber, usually with uneven-aged and multi-levelled canopy; all individuals exhibited strong preference for foraging in old-growth conifer forest (at least 200 years old), with younger forest used progressively less, and forest cleared or burned in preceding 20 years used rarely or not at all; of 1600 roost-sites, 90% were in old-growth forest; of 47 nests studied, 90% in multi-layered old-growth forest, and remainder in stands 70-140 years old with scattered older trees. Possible reasons for species' high dependence on old growth include adequate nest-platform needs, broad temperature gradients and widely diverse roosting sites associated with multi-layered canopy, and associated prey-abundance or prey-availability variables. Occurs from sea-level to c. 2700 m.

Food and Feeding. Small and medium-sized mammals, including e.g. northern flying squirrels (*Glaucomys*), wood rats (*Neotoma*), mice (*Peromyscus*), tree voles (*Phenacomys*), voles (*Microtus*, *Clethrionomys*), snowshoe hares (*Lepus*); also birds, including smaller owls; also frogs, reptiles and insects. Nocturnal, although a roosting owl will opportunistically take prey during day. Hunts from perch, often changing perch several times within single night; detects prey by sight or sound, glides or swoops down and pounces on it, capturing with talons; also snatches arboreal prey from limbs or tree trunks; occasionally hawks for insects and bats. Prey killed on ground or nearby perch by severing cervical vertebrae with bill.

Breeding. Season Mar-Jun. Monogamous. Nest in natural cavity or broken top of tree, or pothole or other cavity in cliff or on cliff ledge, or cave entrance; also in mistletoe brooms or debris accumulation; or uses old squirrel drey or abandoned nest of raptor or corvid; once on ground, 1-4 eggs, usually 2; incubation 30 days, by female, fed by male; female leaves nest briefly to defecate, regurgitate pellets, defend against conspecifics, or receive prey from male; chick covered with white natal down; young brooded and fed by female, food brought by male; as nestlings grow older,

female roosts outside but near nest for more extended periods; fledging 34-36 days. In a summary of 14 studies, 0.25 young fledged/pair for females in their first year, 0.29 for females in their second year, 0.82 for females 3 or more years old; juvenile survival low (0.14-0.26), adult survival high (0.83-0.90). Occasionally breeds in first year; majority of pairs do not breed every year, some known not to breed over periods of 5-6 years. Generally long-lived; in Oregon, several ringed individuals at least 16-17 years old.

Movements. Mostly resident, with some short seasonal shifts. Nominate *occidentalis* sometimes makes short-range seasonal movements (range 15-65 km) or undertakes altitudinal migration (descent 500-1500 m), and *lucida* may also migrate (20-50 km) or move to lower or occasionally higher elevations. In Sierra Nevada, migrates Oct-Dec, spring return generally Feb-Mar; some individuals move back and forth between summer and winter ranges during same winter.

Status and Conservation. Not globally threatened. CITES II. Currently considered Near-threatened. Races *caurina* and *lucida* listed as threatened under US Endangered Species Act, *caurina* as endangered in Canada, *lucida* as threatened in Mexico; *occidentalis* listed as species of special concern by state of California. Status of *caurina* based on historic loss of habitat, projected trends in habitat loss, large areas of low abundance, declining trends in survival rates, and failure of existing regulations to protect race; *lucida* considered threatened in USA owing to projected silviculture strategies and failure of existing regulations to protect it; extensive habitat loss has occurred for both races. In general, nest-sites and prey availability probably serve as limiting factors for population, and primary threats to species include extensive loss of habitat through clear-felling of forest and degradation of habitat due to even-aged tree management; in NW USA, habitat loss ranges from 54% to over 99%. Secondary threats to species include urban and suburban expansion, water development in riparian corridors, agricultural development, fuelwood and oak harvest, reservoir development, and mining activities. In USA, recent management plans for *caurina* criticized by scientists as inadequate; while comprehensive in protection of owl habitat, they lack specific details on owl recovery for either public or private land; in Canada, the Canadian Spotted Owl Recovery Team presented a series of options for *caurina*, most of which contain substantial extinction risk. In California, a current plan for nominate *occidentalis* includes protection of all known sites on federal forest land; however, 2 populations declining and others at serious risk because of low population size, and no listing petition to decrease erosion of habitat or reverse decline of populations. US recovery plan for race *lucida* recommends: protection of 243 ha around nest-sites (or roosting areas if nest-site not known); protection of habitat on steep slopes, natural areas and wilderness areas; changes in logging practices in other habitats (primarily to management for uneven-aged stands); and restoration of, as well as restrictions on use of, riparian zones. Evidence exists that forest selectively logged in past can be reoccupied within 40-100 years if residual elements (snags, coarse woody debris, large trees with cavities) present; however, no published data available for demographic stability in these areas. Also, expanding population of *S. varia* a potential threat to present species, both through predation and because of interbreeding.

Bibliography. Baicich & Harrison (1997), Barrowclough & Gutiérrez (1990), Barrows (1981), Bart (1995), Berbach & Motroni (1994), Bias & Gutiérrez (1992), Blakesley *et al.* (1992), Block *et al.* (1995), Bosakowski (1987), Buchanan *et al.* (1993, 1995), Call & Gutiérrez (1992), Campbell *et al.* (1990), Carey (1995), Carey & Peeler (1995), Carey *et al.* (1992), Clark & Mikkola (1989), Collar & Andrew (1988), Dawson *et al.* (1987), Detrich *et al.* (1993), Dickerman (1997b), Doak (1989), Dunbar *et al.* (1991), Eckert (1974), Ehrlich *et al.* (1992), Everett & Schellhaas (1997), Flora & McGinnis (1991, 1992), Folliard (1993), Forsman & Bull (1989), Forsman & Giese (1997), Forsman, Giese *et al.* (1995), Forsman, Loschl *et al.* (1996), Forsman, Meslow & Wight (1984), Forsman, Sovern *et al.* (1996), Franklin *et al.* (1996), Ganey (1992), Ganey & Balda (1994), Ganey *et al.* (1990), Grubb *et al.* (1997), Gutiérrez (1989, 1996), Gutiérrez & Carey (1985), Gutiérrez & Hunter (1998), Gutiérrez & Pritchard (1990), Gutiérrez, Forsman *et al.* (1996), Gutiérrez, Franklin & LaHaye (1995), Gutiérrez, Seamans & Peery (1996), Hamer *et al.* (1994), Heintzelman (1992), Hof & Raphael (1997), Hopkins *et al.* (1996), Howell & Webb (1995a), Hunter *et al.* (1995), Iverson (1996), Johnson (1988), Kaufman (1996), Kristan *et al.* (1996), LaHaye, Gutiérrez & Akeakaya (1994), LaHaye, Gutiérrez & Call (1992, 1997), Lamberson *et al.* (1994), Lande (1988, 1991), Lehmkuhl & Raphael (1993), Marti (1986), Martin, S.K. *et al.* (1990), Meyer *et al.* (1998), Miller, DeStefano *et al.* (1996), Miller, Small & Meslow (1997), Mills *et al.* (1993), Moen & Gutiérrez (1997), Moen *et al.* (1991), Montgomery (1995), Oberholser (1915b), Paton *et al.* (1991), Pengeroth (1996), Price *et al.* (1995), Raphael *et al.* (1996), Reid *et al.* (1996), Ribe & Morganti (1998), Rinkevich (1995), Rinkevich & Gutiérrez (1996), Ripple & Lattin (1997), Root (1988), Rosenberg *et al.* (1994), Schaldach (1963), Seamans & Gutiérrez (1995), Small (1994), Solis & Gutiérrez (1990), Sovern *et al.* (1994), Steger (1995), Steger & Munton (1997), Stotz *et al.* (1996), Swartz (1914), Tarango (1995), Tarango & Valdez (1997), Thraillkill *et al.* (1996), Tyler & Phillips (1978), Voous (1988), Wagner *et al.* (1996), Walker (1993), Ward *et al.* (1991), White, K. (1996), Wilcove (1987), Williams & Skaggs (1993), Wolfe & de la Torre (1990), Young *et al.* (1997), Zabel, McKelvey & Ward (1995), Zabel, Salmons & Brown (1996), Zhou (1994), Zwick *et al.* (1994).

100. Barred Owl

Strix varia

French: Chouette rayée **German:** Streifenkauz **Spanish:** Cábaro Norteamericano
Other common names: Northern Barred Owl

Taxonomy. *Strix varius* Barton, 1799, Philadelphia, Pennsylvania.

May form superspecies with *S. fulvescens*, possibly also including *S. occidentalis*. Has at times been considered conspecific with *S. fulvescens*, but bigger than nearby populations of latter and with different vocalizations. *S. occidentalis* in Mexico. Four subspecies recognized.

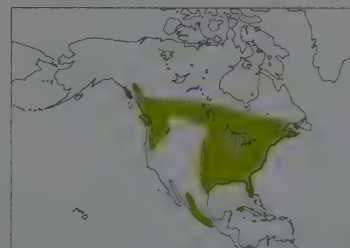
Subspecies and Distribution.

S. v. varia Barton, 1799 - from SE Alaska (possibly) and SW Canada S to N California, E to Nova Scotia, and C & E USA (S to N Texas and North Carolina).

S. v. helveola (Bangs, 1899) - Texas.

S. v. georgica Latham, 1801 - SE USA.

S. v. sartorii (Ridgway, 1874) - mountains of C Mexico (Durango to Oaxaca).



Descriptive notes. Male 48 cm, mean 630 g; female 51 cm, mean 800 g; wingspan 107-111 cm. Rather big owl with large, rounded head. Facial disc grey-white to pale buffy-grey with 4-5 concentric dark rings; crown, neck, chest and most of upperparts brown to grey-brown with narrow buff-white bars; primaries and secondaries barred; tail with 6-7 sharply defined bands of pale brown; belly and flanks buff-white, each feather with broad central stripe of dark brown, undertail-coverts with narrower stripes; tarsus and toes feathered buff-white, marked with numerous but faint bars or spots of brown; iris deep brown; bill pale greenish-

yellow; talons dark horn, deepening to black at tips. Differs from *S. occidentalis* in larger size, streaked (not barred) belly and flanks. Juvenile more red-brown than grey-brown, with buff rather than white barring on hindneck, more pale buff on underparts and on bars of wing and tail. Race *helveola* paler than nominate, especially tail and wings, while *georgica* and *sartorii* considerably darker; all have toes less feathered. Voice. Highly distinctive, far-carrying 9-syllable, 2-phased hoot, transcribable as e.g. "You cook today; I cook tomorrow"; also series of 6-7 barks rising in volume and ending with loud disyllabic hoot; extremely vocal, with shrieks, cries, trills, grumbles and squeaks.

Habitat. Coniferous and mixed deciduous-coniferous forest, usually heavy, mature wood with nearby open country: examples range from thick stands of dense tall pines and hemlock, and well-established hardwood forest, to isolated woodlots with mature and numerous trees, woodland bordering lakes, streams, swamps, marshes or low meadows, and large parks with old trees. In California, found also in coastal redwood (*Sequoiadendron*) and Douglas fir (*Pseudotsuga*) forest. Needs densely foliated trees for daytime roosting, and large trees (at least 50 cm in breast-height diameter) with suitable cavities for nesting; in study in E USA, found to breed significantly closer to forest openings than would be randomly expected, and tended to prefer well-developed understorey and fewer but larger overstorey trees. Apparently can use variety of habitats in both disturbed and undisturbed conditions; will hunt in close proximity to farm buildings, as well as in cities, town dumps and railway yards. From sea-level to upland areas; at 1500-2500 m in Mexico.

Food and Feeding. Mostly small mammals; also birds, fish, reptiles, amphibians and invertebrates; almost without exception, prey that can be swallowed whole. Mammals include e.g. mice, rats, chipmunks, rabbits, bats, moles and opossums; birds include woodpeckers, doves and sparrows, but also crows, domestic poultry and some owl species (*Otus asio*, *Asio otus*); reptiles include tortoises, lizards and snakes; frogs and salamanders known to be taken; also crayfish, scorpions, snails, beetles and grasshoppers. Race *georgica* known to eat young armadillos and baby alligators. Nocturnal, occasionally diurnal. Hunts mostly from perch, flying down on to prey; occasionally hovers; also flushes small birds from their roosts; can strike by sound alone: wades knee-deep in sluggish streams and ponds, snatching prey with the talons and dragging it ashore; occasionally catches bats in flight.

Breeding. Season c. Feb-Aug, depending on region. Monogamous; probably pairs for life. Prefers tree cavity for nest, but will also use abandoned hawk or crow nest, or squirrel drey; in S, nest sometimes between palm fronds; rarely, a scrape on ground; locally, nestboxes used; successful sites used for many years. 2-5 eggs, usually 2-3 (mean 2.41); replacement laid if first clutch destroyed, sometimes third laid if second similarly destroyed; incubation 28-33 days, by female, fed by male; hatching asynchronous; chick covered in fluffy white down; young brooded by female for 3 weeks, may move on to nearby branches at 4-5 weeks, fledge at 6 weeks, cared for by parents for further 2 weeks or more. In one study, 55 broods produced average of 2.02 young. Known to live over 20 years in captivity.

Movements. Mostly resident; more northerly populations sometimes move S, depending on prey availability. In one study, none of 158 ringing recoveries occurred more than 10 km from point of ringing.

Status and Conservation. Not globally threatened. CITES II. Status uncertain; not uncommon locally. Nominate *varia* has expanded W over past 6 decades; now found in W USA and SW Canada, where has successfully colonized a variety of forested and riparian habitats, including old-growth and mature forest; colonization probably facilitated by anthropogenic influences, such as establishment of riparian forest, tree-planting, and creation of mosaic of habitats through logging; expansion could have negative impact on *S. occidentalis* because of potential for hybridization, competition for food and habitat, and predation. Dependent on forest, requires at least some old-growth trees for nesting; has probably suffered in E & SE parts of range, where large stands of mature forest have been lumbered.

Bibliography. Apfelbaum & Seelbach (1983), Applegate (1975), Armstrong (1983), Baicich & Harrison (1997), Baker (1987), Binford (1989), Bird & Wright (1977), Bosakowski (1987, 1994), Bosakowski & Smith (1997), Bosakowski *et al.* (1987), Boxall (1986), Boxall & Stepney (1982), Breedlove (1992), Brock (1994), Campbell *et al.* (1990), Carpenter (1992), Clark (1983), Cook (1992), Dark *et al.* (1998), Devereux (1982), Devereux & Mosher (1982, 1984), Devine *et al.* (1985), Dunbar *et al.* (1991), Dunstan & Sample (1972), Eckert, A.W. (1974), Eckert, K.R. (1997), Ellis *et al.* (1987), Elody & Sloan (1985), Fitzpatrick (1973, 1975), Follen (1986), Forsman & Bull (1989), Fragnier (1995c), Fuller (1979), Gibbs (1988), Hamer *et al.* (1994), Hamerstrom & Janick (1973), Haney (1997), Hawfield (1986), Heintzelman (1992), Holt & Hillis (1987), Howell & Webb (1995a), Ittner (1982), Johnsgard (1979, 1988), Johnson, D.H. (1987), Jones (1987b), Kane & Valent (1986), Kaufman (1996), Laidig & Dobkin (1995), Leder & Walters (1980), Marks *et al.* (1984), Mazur & James (1997), Mazur *et al.* (1998), McGarigal & Fraser (1985), Meshaka (1996), Nero (1993), Nicholls (1973), Nicholls & Fuller (1987), Nicholls & Warner (1972), Peterson (1977, 1989), Price *et al.* (1995), Reichard (1974), Rohweder (1978), Root (1988), Shackelford & Earley (1996), Sharp (1989), Shea (1974), Shupe (1985), Siegfried *et al.* (1975), Small (1994), Smith, D.G. (1980), Smith, D.G. *et al.* (1983), Smith, H. (1989), Soucy (1976, 1997), Stotz *et al.* (1996), Sundquist (1982), Sutton (1988), Sutton & Sutton (1986), Swanson & Liknes (1992), Takats (1996), Taylor & Forsman (1976), Trapp (1989), Tyler & Phillips (1978), Voous (1988), Wolfe & de la Torre (1990), Wright & Hayward (1998), Yannielli (1988, 1991).

101. Fulvous Owl

Strix fulvescens

French: Chouette fauve **German:** Gelbkauz **Spanish:** Cárabo Guatemalteco

Taxonomy. *Syrnium fulvescens* P. L. Sclater and Salvin, 1868, Guatemala.

May form superspecies with *S. varia*, possibly also including *S. occidentalis*. Considered by some to be conspecific with *S. varia*, but differs in vocalizations, morphology and coloration. Monotypic.

Distribution. S Mexico (E Oaxaca and Chiapas), Guatemala, Honduras and El Salvador.



with rhythm "a'hoo a'hoo-hoo a'hoo, hoo"; also single hoots and nasal notes.

Descriptive notes. 38-48 cm. Facial disc pale grey-brown, rimmed dark brown, with short paler eyebrows; crown and upperparts dark brown, coarsely scalloped and spotted with ochraceous-buff; flight-feathers barred buffy and brown; breast buffy with chestnut-brown bars, rest of underparts pale fulvous with broad brown shaft streaks; tarsus and base of toes feathered; iris dark brown; bill bright yellow; toes yellow. Differs from *S. varia* in much smaller size, more rusty upperparts and more tawny underparts. Juvenile ochraceous-buff overall, faintly barred darker above, facial disc brownish. Voice. Loud, barking hoots, often

Habitat. Humid upper tropical and temperate pine-oak forest in mountain zones and cloudforest. Above 1200 m in Honduras; 2200-3100 m in El Salvador.

Food and Feeding. Little information. Diet mainly rodents and insects; also birds, frogs and lizards. Nocturnal; hunts mostly from perch.

Breeding. Young observed in May. Nest in tree hole. 2-5 eggs; incubation 28-30 days, from first egg, by female. No other information.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in North Central American Highlands EBA. Considered uncommon to locally fairly common; species poorly known, however, and status difficult to determine with any reliability. Little available information on species' ecology, but deforestation likely to have detrimental and possibly severe effect on its population size. Occurs in El Triunfo Biosphere Reserve, Chiapas, Mexico.

Bibliography. Anon. (1998a), Binford (1989), Howell & Webb (1995a), Land (1970), Monroe (1968), Ridgely & Gwynne (1989), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Thurber *et al.* (1987).

102. Rusty-barred Owl

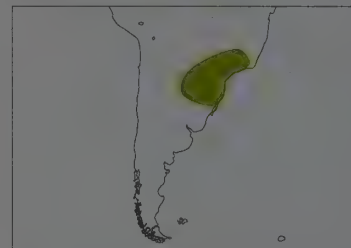
Strix hylophila

French: Chouette dryade **German:** Brasilkauz **Spanish:** Cárabo Brasileño
Other common names: Brazilian Owl

Taxonomy. *Strix hylophila* Temminck, 1825, Ypanema, São Paulo, Brazil.

Thought probably most closely related to *S. chacoensis* and *S. rufipes*, all having vocalizations very different from other *Strix*, and possibly generically distinct. Monotypic.

Distribution. E & S Paraguay, SE Brazil (from Minas Gerais to Rio Grande do Sul) and extreme NE Argentina (Misiones).



Descriptive notes. c. 35 cm; male 285-340 g, female 345-395 g. Facial disc light rusty-brown with broad concentric brown rings and small white eyebrows; upperparts barred with white, brown and orange-buff, scapulars with whitish outer webs; chest and flanks orangish-buff with dark brown bars, belly whiter with similar barring; tarsus feathered; iris blackish-brown; bill greyish with yellow tip; toes pale yellow. Differs from *S. rufipes* in more orange-brown general tone and less uniformly barred breast and belly. Juvenile mostly buff, with diffuse barring. Voice. Deep grunting "grugruu-grugruugruu", first part sometimes

longer, especially in duet; also rolling "rrrrroo", and long-drawn "i-ew-eh"; similar to that of *S. chacoensis*.

Habitat. Montane and tropical lowland evergreen forest, and temperate forest, usually with dense undergrowth; also secondary growth; found both in forest and forest edge, sometimes close to habitation. Lowlands to at least 1000 m.

Food and Feeding. Small mammals, birds and insects; probably also reptiles and amphibians. Nocturnal. Forages in canopy.

Breeding. Season uncertain; possibly Aug-Oct in S, but said also to lay Dec-mid Mar. Nest a hole in tree. 2-3 eggs; incubation 28-29 days, by female, while male hunts for the pair; chick with white down, at 11 days eyes open and wing feathers begin to grow; male reported to help brood young; leave nest at 32-35 days, independent by 4 months. First breeding at 1 year.

Movements. Probably resident.

Status and Conservation. Not globally threatened. CITES II. Generally rare; locally fairly common, e.g. in NE Argentina (Misiones). Major threat appears to be habitat loss, mainly through logging and burning of forest. Because of the scale of such habitat loss in all parts of its range, species should be carefully monitored. Occurs in several protected areas, such as Rio Doce State Park (Minas Gerais) and Aparados da Serra National Park (Rio Grande do Sul) in Brazil, and Iguazú National Park (Misiones) in Argentina.

Bibliography. Belton (1984), Canevari *et al.* (1991), Chebez (1994), Contreras & Contreras (1984), Grummt (1974), Hayes (1995), Lowen, Clay *et al.* (1997), Maurício & Dias (1998), Olog (1968, 1984, 1985), de la Peña (1994), do Rosário (1996), Saibene *et al.* (1996), Schubart *et al.* (1965), Short (1975), Sick (1993, 1997), Stotz *et al.* (1996), Willis (1992).

103. Rufous-legged Owl

Strix rufipes

French: Chouette masquée **German:** Rotfußkauz **Spanish:** Cárabo Bataraz
Other common names: Chilean Spotted Owl, Patagonian Wood-owl

Taxonomy. *Strix rufipes* King, 1828, Port Famine, Straits of Magellan.

Thought probably most closely related to *S. hylophila* and *S. chacoensis*, all having vocalizations very different from other *Strix*, and possibly generically distinct. Usually considered to include *S. chacoensis* as a race, but differs in plumage, morphology and voice. Race *sanborni* described from single immature specimen, perhaps not acceptable. Two subspecies tentatively recognized.

Subspecies and Distribution.

S. r. rufipes King, 1828 - from C Chile and extreme WC Argentina S to Tierra del Fuego.

S. r. sanborni Wheeler, 1938 - Chiloe I, off SC Chile.



Descriptive notes. 33-38 cm. Compact, with large round head. Facial disc rusty with faint concentric dusky rings, white lores and eyebrows; upperparts dark rufous-brown, narrowly barred and spotted orange-buff and whitish; flight-feathers and tail barred buff; throat white, chin barred; underparts buffy-white, heavily barred with blackish, vent uniform orange-buff; tarsus and toes fully feathered buffish; iris dark brown; bill yellowish. Juvenile warm buff, obscurely barred dusky brown, face tawny, many white freckles on head. Race *sanborni* known only from immature specimen: smaller, eyebrows less

prominent. Voice. A series of 10-12 loud, somewhat nasal and high-pitched notes “ú AU ú ú ú...”, with a bouncing effect, introduced by c. 4 dry and low-pitched “brrrr” notes; very different from that of *S. chacoensis*.

Habitat. Dense, moist forest with mosses and lichens, and older secondary growth; more often found in old-growth forest with canopy cover exceeding 75% and heavy understorey, but also occurs in semi-open forest; typical tree species include *Aextoxicum punctatum*, *Gevuina avellana*, *Nothofagus* and *Podocarpus*, in more open habitats sometimes *Araucaria*. Occurs from lowlands to mountain slopes, to at least 2000 m.

Food and Feeding. Specializes on small arboreal mammals, e.g. arboreal mouse (*Irenomys tarsalis*), long-tailed mouse (*Oryzomys longicaudatus*), scansorial black rat (*Rattus rattus*), also colocolo opossum (*Dracopis australis*) and long-haired mouse (*Akodon longipilis*); less frequently, birds (e.g. Furnariidae), amphibians (e.g. Leptodactylidae) and insects (e.g. Blattidae, Scarabaeidae) recorded in diet. In study in S Chile, mammals comprised 94-7% of prey biomass, with birds of minor importance (1-5%) and amphibians negligible (0-5%); although insects outnumbered mammals in the diet during spring and summer, their biomass contribution was unimportant on year-round basis. Nocturnal. Mainly a sit-and-wait predator; probably takes some prey by hawking.

Breeding. Poorly known. Laying probably from Oct. Nest usually in tree hole, occasionally in old raptor nest, possibly rarely on ground beneath cover; 2-3 eggs.

Movements. Resident. Immatures may wander; recorded from Falkland Is (has possibly bred), and 1 report from South Georgia.

Status and Conservation. Not globally threatened. CITES II. Status uncertain, owing to rather elusive habits. 1986 report described species as once common, but appearing to be declining. In mid 1990's in S Chile, first quantitative study reported 0-13 pairs/km in secondary forest and 0-22 pairs/km in old-growth forest, with species closely associated with stands of old timber; predicted that, as forest continues to disappear through logging, the odds for species' long-term survival would decrease. Occurs in several protected areas throughout its range, such as Nahuelbuta and Cerro La Campana National Parks, Chile, and Tierra del Fuego National Park, Argentina. Further research required.

Bibliography. Canevari *et al.* (1991), Fjeldsá & Krabbe (1990), Grigera & Úbeda (1996), Humphrey *et al.* (1970), Johnson (1967), Martínez (1993), Martínez & Jaksic (1995, 1996, 1997), de la Peña (1994), Sayers (1998d), Stotz *et al.* (1996), Straneck & Vidoz (1995), Woods (1988).

104. Chaco Owl

Strix chacoensis

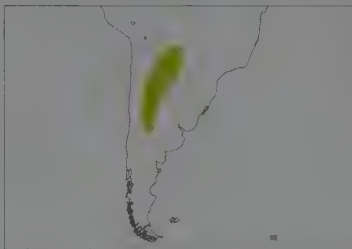
French: Chouette du chaco

German: Chacokauz

Spanish: Cárabo Chaqueño

Taxonomy. *Strix chacoensis* Cherrie and Reichenberger, 1921, Fort Wheeler, Paraguayan Chaco. Thought probably most closely related to *S. hylophila* and *S. rufipes*, all having vocalizations very different from other *Strix*, and possibly generically distinct. Usually treated as race of *S. rufipes*, but differs in plumage, morphology and voice. Monotypic.

Distribution. Chaco of S Bolivia (Santa Cruz), W Paraguay and N Argentina (S to Córdoba, San Luis and N La Pampa).



Descriptive notes. c. 35-40 cm; male 360-435 g, female 420-500 g. Facial disc white with dense dusky rings and dark rim; crown with white-bordered dark central band; upperparts cold dark brown, heavily barred and spotted with white; flight-feathers and tail prominently barred with rufous; underparts whitish, densely barred dark brown; tarsus and toes fully feathered creamy-buff, often with rusty barring; iris dark brown; bill pale yellowish. Differs from *S. rufipes* in longer wings and tail, much paler and colder appearance. Juvenile very pale, diffusely barred. Voice. Deep croaking song, “crucrucru crawl-crawl”, sometimes with extra

“crucru” in middle, last 2 notes louder; female slightly higher, often duets; also single “crawl” notes, and loud “creh-creh-creh” alarm; voice similar to that of *S. hylophila* and very different from that of *S. rufipes*.

Habitat. Dry chaco woodland, usually with large cacti and thorn scrub; avoids open country; said to prefer areas near water.

Food and Feeding. Small mammals, birds and insects (e.g. beetles); also scorpions, large spiders and centipedes; reptiles also recorded, e.g. blind snakes (*Leptotyphlops*). Nocturnal and crepuscular; forages during twilight hours. Hunts from perch.

Breeding. Poorly known; probably lays in Oct; nest in tree hole. In captivity: 3 eggs, incubation 35 days, hatching asynchronous, young left nest at c. 5 weeks.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. No information on population size; probably uncommon, but can be locally fairly common, e.g. Chancaní Provincial Park, Córdoba. Habitat conversion probably main threat. Requires study.

Bibliography. Brooks (1997), Canevari *et al.* (1991), Contreras *et al.* (1990), Fjeldsá & Krabbe (1990), Kratter *et al.* (1993), de la Peña, M.R. (1994, 1997), Short (1975), Steinberg (1998), Stotz *et al.* (1996), Straneck & Vidoz (1995).



105. Ural Owl

Strix uralensis

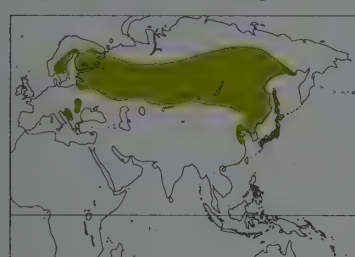
French: Chouette de l'Oural **German:** Habichtskauz **Spanish:** Cárabo Uralense
Other common names: Ural Wood-owl

Taxonomy. *Strix* [sic] *uralensis* Pallas, 1771, Ural Mountains.

Probably forms superspecies with *S. davidi*; usually considered to include latter as a race. Race *liturata* intergrades with nominate *uralensis*. Several additional named races considered inseparable: birds described from Carpathians (*carpathica*) merged with *macroura*; those from L Baikal to W Amurland (*daurica*), from Sakhalin (*itabanae*) and from NE China and Korea (*corensis*) merged with *nikolskii*; those from C Honshu (*nomiyamae*) included in *hondoensis*. Eight subspecies recognized.

Subspecies and Distribution.

- S. u. liturata* Lindroth, 1788 - N Europe and NW Russia (E to about Arkhangel'sk region), S to N Poland, Belarus and middle R Volga.
- S. u. uralensis* Pallas, 1771 - from E European Russia E to Okhotsk coast.
- S. u. macroura* Wolf, 1810 - C & SE Europe (from Carpathian Mts S to Bulgaria, and in W Balkans).
- S. u. yenisseeensis* Buturlin, 1915 - C Siberian plateau.
- S. u. nikolskii* (Buturlin, 1907) - Transbaikalia E to Sakhalin, S to NE China and Korea.
- S. u. japonica* (Clark, 1907) - Hokkaido.
- S. u. hondoensis* (Clark, 1907) - N & C Honshu.
- S. u. fuscescens* Temminck & Schlegel, 1847 - S Honshu S to Kyushu.



whitish to pale grey-brown, streaked dark, vent plain white; tarsus and toes fully feathered; eyes relatively small, iris dark brown; bill yellow. Differs from *S. nebulosa* in smaller size, dark eyes, lack of facial rings. Juvenile facial disc pale, head feathers heavily tipped white, appearing pale-headed; underbody grey, barred brown. Racial variation mostly slight: *liturata* darker than nominate; *macroura* darker still, larger; *nikolskii* tinged brownish; *fuscescens* much smaller, rufous-brown; *japonica* very pale. **VOICE.** Usually fairly silent; male advertising call "Hu-ooo, Hooo hu-HOO-hoo", with c. 15-50 seconds between calls; female similar but much harsher; duets during courtship; also, harsh "craaw" and series of barks.

Habitat. Boreal forest and mixed woodland, with some open areas such as bogs, clearings or small fields; often found near human dwellings, either in use or abandoned, and also pastures; in S of range (C Europe), confined to deciduous woods, especially of beech (*Fagus sylvatica*), in mountain areas. Hunts in forest glades and fringes of woods; in winter also in other open areas, including parkland and occasionally in vicinity of villages. Generally in lowlands; in C Europe breeds at 450-850 m in Slovakia, to tree-line at 1100-1200 m in Carpathians, and to 1600 m in Romania; in Japan to 1600 m in Honshu, Kyushu and Shikoku, only in lowlands in Hokkaido.

Food and Feeding. Mammals, from size of small rodents such as mice and voles (Microtinae), to larger ones such as water voles (*Arvicola*) and young hares (*Lepus*); also birds, from size of finches (Fringillidae) to pigeons (*Columba*) and Black Grouse (*Tetrao tetrix*); occasionally amphibians, lizards and insects; will also take carrion. In Finland, mammals comprised 86% of prey by number and 87% by weight, vast majority being voles (*Microtus*); birds 9% of prey by number and 11% by weight, with passerines the most important; frogs constituted 5% of prey by number. Nocturnal, occasionally diurnal; most active around dusk and just before dawn. Most hunting from perch; probably also uses searching flight; prey detected by sound, can locate rodents under 20-30 cm of snow. Larger prey decapitated before given to nestlings; surplus food stored at or near nest.

Breeding. Season Feb-Jul. Monogamous; 1 known case of polygyny; pairs usually for life, divorce rate less than 3%. Nest in tree hole or hollow stump, sometimes cavity in cliff or building, often in nestbox; sometimes in old nest of raptor (*Accipiter*, *Buteo*, *Pernis*), crow (*Corvus*) or squirrel (*Sciurus*); rarely on ground; no material added; of 250 Finnish nests (1870-1969), 33% in nestbox, 28% in old nest of other species, 28% in stump, 9% in hole in tree, 1% in building, 0.5% on ground and 0.5% on rock face; high nest-site fidelity; large territory, c. 10 km² in ideal habitat. 2-4 eggs, occasionally 1-6, laying interval 1-3 days; incubation 28-34/35 days, by female, fed by male; hatching asynchronous; chick covered in white down; young brooded up to 2 weeks, by female, latter more fierce than male in nest defence; young leave nest at c. 35-40 days, can fly at c. 45 days, remain with parents for further 2-3 months. In Sweden, of 203 eggs, 80% hatched, with most losses due to food shortage causing female to cease incubation, and of 162 young hatched 98% fledged, giving overall productivity of 0.78 young/eggs laid; in Finland, factors affecting lifetime reproductive success thought to be female body size and nest defence, laying dates (more successful early in season), territory quality, prey populations, and snow cover (affecting access to prey). Age of first breeding usually 3-4 years, although individual ringed as nestling laid eggs at 11 months. Longevity record of ringed individual 20 years, but some probably survives longer.

Movements. Mainly resident, even sedentary. Nearly all males and 90-95% of females stay near previous nest-sites, even during least favourable years; in harsh winters, some females move 100-150 km away from territory and, if they survive, sometimes totally change their breeding area; autumn and winter wandering apparently more extensive in W & C Siberia. Young disperse Sept-Nov; in Finland, two-thirds of first-year birds dispersed within 30 km of natal site, although up to 200 km recorded.

Status and Conservation. Not globally threatened. CITES II. European population estimated at c. 11,000-14,000 pairs (excluding Russia) in mid 1990's, including 4000 in Finland, 4000 in Sweden and 2500 in Estonia; surprisingly high maxima elsewhere, e.g. 2000 pairs in Latvia, 1200 pairs in Belarus, and 1000 pairs in Romania where formerly thought rare. Modern forestry practice of removing old trees and chimney-like stumps a severe threat in Fenno-Scandia, causing decrease in

population, but provision of thousands of nestboxes has led to recovery and even increase; in S Finland current density up to 6-7 pairs/100 km² usual, but in optimum habitat up to 10 pairs/100 km²; considered relatively stable in Fenno-Scandia, but without such artificial sites will probably decline in the future. No reliable data from rest of range, but Russia probably holds substantial population; in former USSR, some fluctuation reported, with earlier decreases in Belarus (1967) and Bashkiriya (1979). In Japan, considered a fairly common resident, although at apparently low density. Population levels partly dependent on food supply, as shortages, especially of small mammals, inhibit breeding (and can provoke irruptive movements). Across range of nominate *uralensis*, reproduction runs fairly parallel to cyclic fluctuations of voles; after hatching, vole abundance perhaps less crucial since declining vole populations compensated for by increased predation on returning migratory birds; breeding success largely regulated by vole availability in winter and early spring; also, clutch size can be partly explained in terms of food limitation.

Bibliography. Beaman (1994), Beaman & Madge (1998), Becker & Pieper (1982), Bessy (1976), Brazil (1991), Brazil & Yamamoto (1989a), Brommer *et al.* (1998), Cramp (1985), Eriksson *et al.* (1984), Etchécopar & Hue (1978), Flint *et al.* (1984), Forsman (1998), Gorman (1995), Hagemeijer & Blair (1997), Hakkarainen & Korpiamäki (1996a), Holmberg (1974), Jaderholm (1987), Janosy *et al.* (1992), Kazama (1974), Knystautas (1993), Kohl & Hamar (1978), Korpiamäki (1986b, 1992a), Korpiamäki & Huhtala (1986), Korpiamäki & Sulkava (1987), Korpiamäki *et al.* (1990), Kunysz (1989), Lahti (1972), Lundberg (1974, 1976, 1979, 1980a, 1980b, 1981), Lundberg & Westman (1984), Mikola (1972, 1983), Minnemann & Busse (1978), Nishimura (1988, 1991), Nishimura & Manabu (1988), Parusel (1993), Petrovics (1995), Pietiäinen (1988, 1989), Pietiäinen & Kolonen (1986, 1993), Pietiäinen, Saurala & Kolonen (1984), Pietiäinen, Saurala & Väisänen (1986), Rogacheva (1992), Saurala (1980, 1987, 1989a, 1989b, 1991, 1992, 1997), Schäffer (1990), Scherzinger (1974b, 1981, 1983, 1987), Simeonov *et al.* (1990), Snow & Perrins (1998), Solheim & Bjørnstad (1987), Stepanyan (1990), Turk (1996), Volcan & Pedrini (1988), Volkov *et al.* (1998), Voous (1988), Wang Sung (1998), Yoneda *et al.* (1979), Zhao Zhengjie (1995).

106. Sichuan Wood-owl

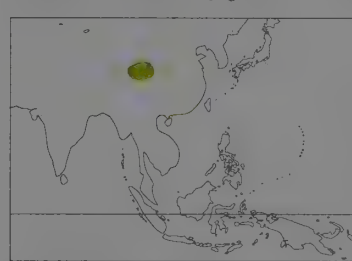
Strix davidi

French: Chouette du Sichouan **German:** Sichuankauz **Spanish:** Cárabo de Sichuán
Other common names: Pere David's Owl/Wood-owl

Taxonomy. *Syrnium davidi* Sharpe, 1875, Mupin, Sichuan.

Probably forms superspecies with *S. uralensis*; usually treated as conspecific with latter on basis of vocal similarities, but separated by morphological differences and geographical isolation; further study needed. Monotypic.

Distribution. C China: SE Qinghai and W & C Sichuan.



Descriptive notes. c. 58 cm. Facial disc with indication of dark concentric rings, and distinct dark border; upperparts rich brown, mottled with blackish-brown, grey and white, greater coverts tipped white and with broad black subterminal bar; flight-feathers and tail barred brown and dusky; breast and belly heavily streaked with black-brown; iris brown; bill pale yellow. Differs from *S. uralensis* in darker appearance, with markings much darker and better defined than any race of latter. Juvenile undescribed. **VOICE.** Long, quavering hoot; barking "khou-khou"; also harsh "ke-wick".

Habitat. Coniferous and mixed forest with

adjacent open areas, from 4000 m to 5000 m.

Food and Feeding. No information.

Breeding. No information.

Movements. Resident.

Status and Conservation. **VULNERABLE.** CITES II. Restricted-range species; present in West Sichuan Mountains EBA. Apparently rare, but no quantitative data on population. Occurs in Jiuzhaigou Reserve, Sichuan. Threatened by extensive deforestation occurring within its range. Further research urgently required.

Bibliography. Beaman (1994), Cheng Tsohsin (1987), Collar *et al.* (1994), Etchécopar & Hue (1978), Inskipp *et al.* (1996), Meyer de Schauensee (1984), Stattersfield *et al.* (1998), Wang Sung (1998), Zhao Zhengjie (1995).

107. Great Grey Owl

Strix nebulosa

French: Chouette lapone **German:** Bartkauz **Spanish:** Cárabo Lapón
Other common names: Dark Wood-owl; Lapland Owl/Striped Owl, Lapp Striped Owl (*lapponica*)

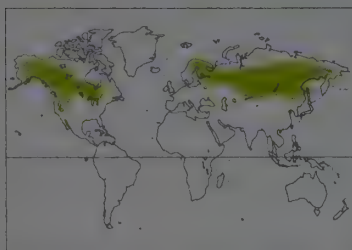
Taxonomy. *Strix nebulosa* J. R. Forster, 1772, northwestern Ontario, Canada.

Affinities uncertain. Population from Kentei Mts, in N Mongolia has been separated as *elisabethae*, but doubtfully separable from *lapponica*. Two subspecies recognized.

Subspecies and Distribution.

- S. n. nebulosa* J. R. Forster, 1772 - North America, from C Alaska E to SW Quebec, S to EC California, N Idaho and NE Minnesota.
- S. n. lapponica* Thunberg, 1798 - Eurasia, from Fenno-Scandia E to W Koryakland, S to Lithuania, N Mongolia, NE China and N Sakhalin.

Descriptive notes. 59-69 cm; male c. 800-1175 g, female 925-1700 g. Large owl, with big rounded head and small, "staring" eyes; slow, deep wingbeats in flight. Facial disc large, circular, light grey with 6 or more concentric rings of darker grey or brown, with whitish eyebrows and lores, and black chin with white at sides; upperparts dark grey to grey-brown, fading with age to brown, with transverse mottling of greyish-white and dark, and some dark streaks; wings and tail barred dark and light grey; underparts greyish with faint vermiculations, broadly streaked with dark grey; tarsus and toes thickly feathered grey; iris and bill yellow. Juvenile cryptic grey and white. Race *lapponica* often somewhat paler than nominate, underparts whiter and more clearly streaked, vermiculations very faint. **VOICE.** Series of low, evenly spaced "hoou" notes, deep and booming, accelerating and dropping slightly near end; female higher-pitched, hoarser; this call typically given most frequently during breeding and near nest; also low, soft double hoots, possibly contact call associated with territorial defence.



Habitat. Dense boreal or coniferous forest, favouring areas with openings; taiga interspersed with sphagnum bogs, muskeg or open fields; pine and fir forest adjacent to montane meadows; and tamarack, black spruce and aspen forest. Outside breeding season occasionally occurs in other habitats, too, sometimes near habitation. Forages mostly at forest edge or in open areas with clear view. Sea-level to c. 1000 m; in California to 2400 m. In Utah to 3200 m.

Food and Feeding. Small mammals, especially rodents; also birds up to size of grouse (Tetraonidae), and frogs and large insects. During breeding, largely voles (*Microtus*).

which often form 90% or more of diet; other mammals include mice, squirrels and hares, and shrews often taken in winter; recorded killing Sharp-shinned Hawk (*Accipiter striatus*). Nocturnal and crepuscular, sometimes diurnal. Hunts from perch, listening and watching ground; after detecting prey, flies up to 100 m to strike. Can detect prey beneath snow by sound alone; will hover, plunge face downward, break through snow cover with "clenched" feet, and grab prey with feet and talons; able to break through snow crust hard enough to support an 80-kg weight, and as deep as 45 cm. Small mammals swallowed whole; larger prey pulled into pieces.

Breeding. Season Mar-Jul in North America; Mar-Aug in Europe. Monogamous; occasional polygyny suspected; pair-bond not maintained over winter, but may nest with same mate in subsequent year if prey populations remain high; pairs form as early as Jan, or as late as 2 weeks prior to laying. Lays in abandoned nest of other bird of prey, or on broken tree snag, sometimes on mistletoe broom, or rarely in shallow depression at foot of tree; also uses artificial platforms; no material added; territory size variable depending on food and site, 0.5-25 km². Male sometimes performs aerial displays, 2-9 eggs, usually 3-5, depending on food supply, laying interval 2 days; clutch sometimes replaced if first lost; incubation c. 28-36 days, by female, fed on nest by male, females leaving very occasionally and briefly to defecate and regurgitate pellets; hatching asynchronous; chick with whitish-grey down; young leave nest at 25-30 days, unable to fly, readily climb leaning trees and roost off ground, capable of flight 7-14 days later; after fledging, young fed directly by male. In NE Oregon, of 67 nesting attempts monitored, 78% fledged young; in Idaho and Wyoming 70-5%, in Manitoba and Minnesota 81%; in Oregon, probability of juvenile surviving first year 0.53, first two years 0.3. Age of first breeding most commonly 3 years, rarely 1, occasionally 2. Can be long-lived: female ringed as adult recaptured 13 years later; has reached 27 years in captivity.

Movements. Resident and nomadic; movement patterns variable, stable in some areas and/or years, highly irruptive in others, influenced by prey availability. Both altitudinal and latitudinal movements occur. Birds probably move also to avoid deep snow, although known to winter well N (as well as S) of its taiga breeding range in Russia. Irrupts into areas with abundant food supply (voles), occasionally breeding in such places well outside normal range. In North America, wanders S to NE Wisconsin and N Michigan; in Europe, has reached N Germany and Ukraine. When migrating, can occur in loose concentrations, probably in response to abundant prey.

Status and Conservation. Not globally threatened. CITES II. Populations fluctuate widely, but generally scarce, with food supply likely critical factor regulating numbers: in Sweden, numbers of pairs breeding vary from 0 to 100 or more in any year, with highest total nests recorded 76 in 1981; in Finland after late 1930's, apparently almost extinct for over 20 years, but since mid 1960's population in peak years several hundreds of pairs, following 3- to 4-year rodent cycle. Population of Europe (excluding Russia) in "normal" years estimated at 500-1500 pairs in 1990's; in Finland minimum of 850 pairs, but possibly 1000-1600 pairs in good vole years. In Russia, marked fluctuations, often scarce: 1 pair/km linear density in Arkhangelsk area; typically 0.05-0.1 birds/km² in Komi Republic, but 0.3 birds/km² in peak vole year; mean overall density in Perm region found to be as low as 0.3 pairs/1000 km²; said to be common in E Siberia. Extremely rare in China. North American population estimated at minimum of 50,000 individuals. Potential threats identified in North America include timber-harvesting, which reduces number of large-diameter trees (live and dead) for nesting, leaning trees used by juveniles for roosting before they can fly, dense canopy closures used by juveniles for cover and protection, and perches required for hunting; also, collisions with automobiles a major cause of mortality in some years; strychnine poisoning of pocket gophers potential harmful; development of campgrounds and associated disturbances may have eliminated species' hunting areas in Yosemite National Park, in California; grazing could reduce prey populations; forestry, peat extraction and agriculture possible threats to preferred habitats in Manitoba. Provision of artificial nest structures (wire baskets or wooden platforms with sticks placed on top) enhances local breeding, with success 83% on artificial platforms versus 66% at natural sites (old stick nests); also allows occupation of new habitats, suggesting that nest-sites a key limiting factor. In USA, known nest-sites protected from logging (National Forest Service land); in some areas, recommended management guidelines include restricted harvest unit size, retention of hunting perches in cut-over areas, and irregularly shaped harvest units (Manitoba and Minnesota). Modified forest management could also enhance habitat by opening up dense forest stands.

Bibliography. Albertini (1996), Armstrong (1983), Atkinson (1989), Baicich & Harrison (1997), Beaman & Madge (1998), Beck & Smith (1987), Berggren & Wahlstedt (1977), Bouchart (1991), Bruntton & Pittaway (1971), Bruntton & Reynolds (1984), Bryan & Forsman (1987), Bull (1989), Bull & Duncan (1993), Bull, Henjum & Anderson (1987), Bull, Henjum & Rohweder (1988a, 1988b, 1989a, 1989b), Campbell *et al.* (1990), Cramp (1985), Cyr (1995a), Duncan (1987, 1992, 1997), Eckert, A.W. (1974), Eckert, K.R. (1997), Etchecopar & Hue (1978), Fisher (1975), Flint *et al.* (1984), Follen (1980, 1984), Forsman, D. (1998), Forsman, E.D. & Bull (1989), Franklin (1988), Goggans & Platt (1992), Groves & Zehntner (1990), Hagemeier & Blair (1997), Harris (1984), Hayward & Verner (1994), Heintzelman (1992), Hilden & Holo (1981), Hilden & Solonen (1987), Hoffmann (1992), Johngard (1979, 1988), Kaufman (1996), Korpimäki (1986b, 1992a), Lang *et al.* (1991), Lonikowski *et al.* (1989), Mikko (1981, 1983), Munts & Powers (1991), Nero (1984, 1985, 1986, 1991), Nero & Copland (1981), Nero & Loeh (1984), Nero *et al.* (1984), Osborne (1987), Pulliainen & Kalevi (1977), Randklev & Randklev (1996), Reinhard (1981), Rogacheva (1992), Servos (1987), Small (1994), Snow & Perrins (1998), Solonen (1986), Spreyer (1987), Stehrbakov (1990), Stefansson (1979, 1983, 1986), Stepanyan (1990), Sulkava & Huhtala (1997), Tyler & Phillips (1978), Volkov *et al.* (1998), Voous (1988), Wahlstedt (1976), Walker (1993), Wang Sung (1998), Wheat (1979), Wildman (1992), Wolfe & de la Torre (1990), Zakharov (1991), Zhao Zhengjie (1995).

108. African Wood-owl

Strix woodfordii

French. Chouette africaine **German:** Afrikanischer Waldkauz **Spanish:** Cárabo Africano
Other common names: Woodford's Owl

Taxonomy. *Noctua Woodfordii* A. Smith, 1834, Knysna, Cape Province.

This species, along with Neotropical *S. virgata*, *S. nigrolineata*, *S. huhula* and *S. albitarsus*, sometimes placed in separate genus *Ciccaba* on basis of differences in external ear structure compared with *Strix*, but DNA studies show that generic separation not warranted. Birds from Sokoke Forest in Kenya sometimes separated as *sokokensis*; populations described from Central African Republic to Sudan and S Zaire (as *bohndorffi*) considered not separable from other races. Four subspecies recognized.

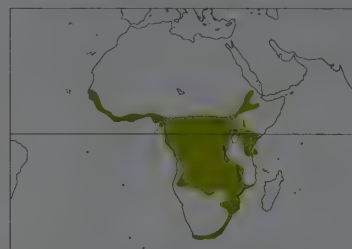
Subspecies and Distribution.

S. w. nuchalis (Sharpe, 1870) - Senegambia E to S Sudan and Uganda, S to N Angola and Zaire (except S & E), including Bioko I.

S. w. umbrina (Heuglin, 1863) - Ethiopia and SE Sudan.

S. w. nigricantior (Sharpe, 1897) - S Somalia, Kenya, Tanzania, Zanzibar and E Zaire.

S. w. woodfordii (A. Smith, 1834) - S Angola and S Zaire E to SW Tanzania, S to N Botswana and the Cape.



Descriptive notes. 30-36 cm; wingspan 80 cm; male 240-270 g, female 285-350 g. Medium-sized owl with large, round head. Buff facial disc, darkest around eyes, prominent white eyebrows; rest of head dark rufous-brown, spotted with white; upperparts dark rufous-grey, spotted and streaked white and buff, scapulars with white outer webs; flight-feathers and tail barred; breast rufous with thin white bars, rest of underparts barred rufous and white; tarsus feathered buff, barred brown; iris dark brown, eyelids red; bill yellow; toes yellowish. Juvenile paler rufous with white bars, facial markings less pronounced; indistinguishable from adult by 5 months. Races

separated by tone of russet colour and by amount of barring on breast: *nuchalis* brightest russet, broadest white chest bars; *nigricantior* more blackish; *umbrina* more brown, with more extensive white barring below. **Voice.** Series of rapid hoots, "who-who who-uh-uh who-oo", first part louder, rest in varying rhythms; female higher-pitched; also high "wheow" by both, male and female; sometimes duets.

Habitat. Woodland and forest, from dense montane forest to bush and riparian areas, coastal forest and lowland rainforest; also inhabits plantations. From sea-level to 3700 m.

Food and Feeding. Varied diet: mainly insects, including katydids, grasshoppers, crickets, cicadas, mantises, cockroaches, moths and caterpillars; also reptiles, frogs and birds, the last including kingfishers (Alcedinidae) as well as small passerines; also small mammals, e.g. rodents and shrews. Nocturnal; occasionally seen by day. Hunts by dropping on to prey from low perch, often 1-2 m from ground; occasionally catches insects in flight, or gleans them from vegetation.

Breeding. Lays Jul-Oct, peak in Sept; Oct-Feb in W Africa. Nest in natural cavity or broken tree top, 2-30 m above ground, usually 2-4 m; rarely at base of tree, under log in leaf litter; 2 accounts of using old nest of goshawk (*Accipiter*); same site re-used even if pair-members change; territory small, c. 50 ha, defended vigorously, 1-3 eggs, usually 2, laying interval 2-4 days; incubation c. 31 days, by female, fed by mate; hatching asynchronous; chick with white down; nestlings brooded by female continuously for 3 weeks, female then helps male in hunting; young leave nest at 30-37 days, sometimes earlier, stay near nest in shelter, can fly at c. 46 days; young remain within parental territory up to 4 months, sometimes do not leave until onset of next breeding cycle, when parents evict them. Genets (*Genetta*) suspected nest predators; pairs with early failures may re-lay.

Movements. Resident.
Status and Conservation. Not globally threatened. CITES II. Commonest owl of forest and woodland throughout whole of sub-Saharan Africa. Occurs in a considerable number of protected areas in most countries throughout its extensive range. No known threats, although habitat destruction could possibly be a problem locally; often seen on roadsides after dark, so some traffic casualties likely.

Bibliography. Allen & Ballantyne (1980), Ash & Miskell (1998), Bannerman (1953), Barlow *et al.* (1997), Benson & Benson (1977), Benson *et al.* (1971), Carlyon & Meakin (1986), Cave & Macdonald (1955), Cheke & Walsh (1996), Colston & Curry-Lindahl (1986), Cunningham-van Someren (1975), Dean & Macdonald (1971), Delpont *et al.* (1998), Dowsett (1990), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Elgood *et al.* (1994), Field (1998), Fry *et al.* (1988), Gatter (1997), Ginn *et al.* (1989), Grimes (1987), Harrison *et al.* (1997), Harvey (1977), Haugaard (1996), Hockey *et al.* (1989), Kemp & Calburn (1987), Kemp & Kemp (1989, 1998), Lambour & Steyn (1986), Lewis & Pomeroy (1989), Mackworth-Præd & Grant (1957, 1962, 1970), Maclean (1993), Manson (1982), Marchant (1948), Nieboer & van der Paardt (1977), Pakenham (1979), Penry (1994), Pickford *et al.* (1989), Pinto (1983), Scott (1980), Short *et al.* (1990), Snow (1978), Steyn (1982, 1984, 1994a), Steyn & Scott (1973), Vernon (1980), van der Weyden (1972), Zimmerman, D.A. (1972), Zimmerman, D.A. *et al.* (1996).

109. Mottled Owl

Strix virgata

French: Chouette mouchetée **German:** Sprenkelkauz **Spanish:** Cárabo Café
Other common names: American Wood-owl

Taxonomy. *Syrnium virgatum* Cassin, 1849, Bogotá.

This species, along with *S. nigrolineata*, *S. huhula*, *S. albitarsus* and sometimes Afrotropical *S. woodfordii*, often placed in separate genus *Ciccaba* on basis of differences in external ear structure compared with *Strix*, but DNA studies show that generic separation not warranted. W Colombian birds sometimes separated as race *minuscule*. Seven subspecies recognized.

Subspecies and Distribution.

S. v. squamulata (Bonaparte, 1850) - W Mexico (Sonora to Guerrero and Guanajuato to Morelos).

S. v. tamaulipensis Phillips, 1911 - NE Mexico (S Nuevo Leon and Tamaulipas).

S. v. centralis (Griscom, 1929) - E & S Mexico to W Panama.

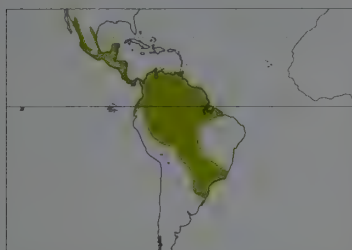
S. v. virgata (Cassin, 1849) - E Panama, Colombia, Ecuador, Venezuela and Trinidad.

S. v. macconnelli (Chubb, 1916) - the Guianas.

S. v. supercilialis (Pelzelin, 1863) - NC & NE Brazil.

S. v. borelliana (W. Berton, 1901) - SE Brazil, E Paraguay and NE Argentina (Misiones).

Descriptive notes. 29-38 cm; 175-320 g. Occurs in light and dark morphs, found in drier and humid areas respectively. Light morph with brown facial disc with bold white eyebrows, lores and whiskers; dark brown above with faint whitish barring, scapulars with white outer webs; whitish to pale buff below, mottled dark brown on chest, rest of underparts streaked dark brown; tarsus feathered; iris dark brown; bill yellow-grey to blue-grey; toes grey to yellowish. Dark morph somewhat darker all over, upperparts vermiculated greyish-buff to ochraceous-buff, underparts with deep buff ground colour, some dark-morph individuals very black. Juvenile mostly buffy to cinnamon, barred with dusky above, facial area whitish, bill pinkish; like *Pulsatrix*, has series of immature plumages. Races vary in pattern of markings, those in N parts of range smaller with fine distinct barring above, those in Amazon larger and more reddish-brown: *squamulata* smaller than nominate, more spotted above; *centralis* more barred above; *macconnelli* somewhat barred below; *superciliaris* larger, more rufous; *borelliana* dark, pale



markings more buff. Voice. Common territorial call a series of deep, short, frog-like hoots, "gwho gwho gwho...", increasing in pitch and volume, then decreasing; sometimes single hoot, or 1-3 grunts alone; female call cat-like.

Habitat. Wide variety of forest and thickly edge: tropical rainforest, tropical dry lowland forest, pine-oak woodland, thorn forest, gallery forest, semi-open areas and second growth, coffee and cacao plantations, and areas with scattered trees; often close to towns and villages, even in cities. Sea-level to 2500 m.

Food and Feeding. Varied diet suggests opportunist: large insects such as beetles, cockroaches and grasshoppers; small mammals (*Oryzomys fulvescens*, *Sigmodon hispidus*, *Otiotylomys phyllotis*), also bats; small reptiles, including snakes, salamander, lizards (*Anolis*); also tree frog (*Hyla*); probably some small birds. Strictly nocturnal. Forages along forest edge; hunts from perch; probably takes some insects in flight; sometimes attracted to artificial lights.

Breeding. Lays Feb-Apr in Central America, nest with eggs found in Jun in S Mexico (Oaxaca); lays Feb-May in Colombia, Sept-Nov in S of range; juveniles Feb-Mar in NE Argentina. Nest usually in hole of live tree (*Pimenta dioica*, *Brossium alicastrum*) or palm stub; sometimes uses old nest of another bird. 1-2 eggs; no information on incubation or fledging.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Rather widespread, and considered fairly common to common in some places; reportedly common in S Mexico in lowlands, uncommon in Osa Peninsula (Costa Rica), and fairly common from Panama to Colombia and Venezuela; locally not uncommon in S of range; little information, however, on relative abundance in many places. Occurs in a considerable number of protected areas throughout its extensive range. Ecology fairly unknown for such a common species; needs at least patchy forest. Loss of habitat and further forest fragmentation may affect its population; road casualties not infrequent.

Bibliography. Binford (1989), Bonilla *et al.* (1992), Canevari *et al.* (1991), Gerhardt (1991), Gerhardt, Bonilla *et al.* (1994), Gerhardt, Gerhardt *et al.* (1994), Haverschmidt & Mees (1994), Hayes (1995), Herklots (1961), Hilty & Brown (1986), Howell & Webb (1995a), Land (1970), Lasley *et al.* (1988), Lowery & Dalquest (1951), Meyer de Schauensee & Phelps (1978), Miller (1963), Monroe (1968), Olrog (1985), de la Peña (1994), Ridgely & Gwynne (1989), Rowley (1984), Saibene *et al.* (1996), Schaldach (1963), Sick (1993, 1997), Slud (1964), Snyder (1966), Stiles & Skutch (1989), Stotz *et al.* (1996), Tostain *et al.* (1992), Voous (1988), Wetmore (1968a), Wyllie (1976).

110. Black-and-white Owl

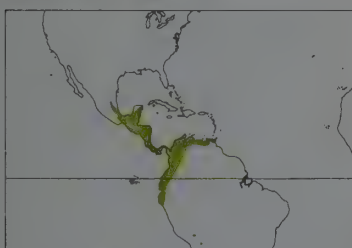
Strix nigrolineata

French: Chouette à lignes noires **German:** Bindenhalskauz **Spanish:** Cárabo Blanquinegro

Taxonomy. *Ciccaba nigrolineata* P. L. Selater, 1859, Oaxaca, Mexico.

This species, along with *S. virgata*, *S. huhula*, *S. albitarsus* and sometimes Afrotropical *S. woodfordii*, often placed in separate genus *Ciccaba* on basis of differences in external ear structure compared with *Strix*, but DNA studies show that generic separation not warranted. Forms superspecies with *S. huhula*. Sometimes considered conspecific with latter, but bigger, with significant differences in plumage and voice. Monotypic.

Distribution. C Mexico to NW Venezuela, W Colombia and W Ecuador and extreme NW Peru.



Descriptive notes. 33-45 cm; male c. 435 g, female c. 535 g. Facial disc black with indistinct white-speckled border, eyebrows speckled white; crown blackish, broad white-spotted nuchal band; upperparts sooty-brown; tail thinly banded white; underparts white, all evenly and narrowly barred with dark brown; tarsus feathered whitish with dark bars; iris dark brown; bill yellow; toes orange-yellow. Juvenile face whitish, white closely barred with dark brown above, wing-coverts black with some white barring, below buffy-white with dark bars. Voice. Barking hoots, "hu whoOOO"; also series of 3-5 or more notes, last or penultimate note emphatic, "who-who-WHOW-woh".

Habitat. Humid forest, semi-deciduous and deciduous forest, edges and clearing, gallery forest, tall mangroves, plantations, woodland near rivers or swamps; sometimes near villages. Sea-level to 1200 m in Mexico, to 2100 m in Panama, and to 2400 m in Colombia.

Food and Feeding. Insects, such as coleopterans (most commonly Scarabaeidae), orthopterans (Blattellidae), Tettigoniidae, Curculionidae, Cerambycidae; also small vertebrates, including bats (*Artibeus jamaicensis*, *Myotis nigricans*, *Molossus ater*, *Centurio senex*, *Uroderma bilobatum*), rodents (*Oryzomys fulvescens*), possibly also birds. Nocturnal. Hunts from perch; also takes bats and insects in flight, sometimes near artificial lights.

Breeding. Lays late Mar-May, during dry season. Nest in tree hole, or sometimes among epiphytes (*Phylladendron*, *Tillandsia*) or orchids (*Mormolyca ringens*, *Trigonidium egeronianum*) on large and living trees; said occasionally to use old stick nest. 1-2 eggs.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Considered uncommon to fairly common in Mexico; apparently widely distributed but scarce in Honduras; reported as uncommon to rare in Costa Rica; rare in Panama; very local and rare in Colombia and Venezuela, but regularly recorded at Henri Pittier National Park (Aragua). Probably overlooked. Forest clearance a likely threat; extensive use of pesticides may also affect it.

Bibliography. Anderson *et al.* (1998), Beck (1990), Binford (1989), Blake (1958), Gerhardt, Bonilla *et al.* (1994), Gerhardt, Gerhardt *et al.* (1994), Hilty & Brown (1986), Howell & Webb (1995a), Ibañez *et al.* (1992), Kirwan & Sharpe (1999), Land (1970), McCarthy (1976), Meyer de Schauensee & Phelps (1978), Monroe (1968), Orians & Paulson (1969), Ridgely & Gwynne (1989), Slud (1964), Stiles & Skutch (1989), Stotz *et al.* (1996), Thurber *et al.* (1987), Wetmore (1968a), Willis & Eisenmann (1979).

111. Black-banded Owl

Strix huhula

French: Chouette huhul **German:** Zebrakauz **Spanish:** Cárabo Negro

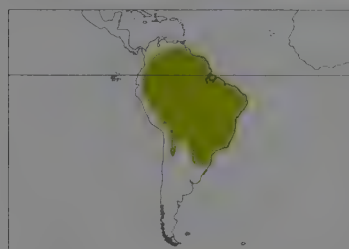
Taxonomy. *Strix huhula* Daudin, 1800, Cayenne.

This species, along with *S. virgata*, *S. nigrolineata*, *S. albitarsus* and sometimes Afrotropical *S. woodfordii*, often placed in separate genus *Ciccaba* on basis of differences in external ear structure compared with *Strix*, but DNA studies show that generic separation not warranted. Forms superspecies with *S. nigrolineata*. Sometimes treated as conspecific with latter, but differs in size, voice and plumage. Two subspecies recognized.

Subspecies and Distribution.

S. h. huhula Daudin, 1800 - E Colombia, S Venezuela and the Guianas to NE Brazil, S to E Peru, NW Argentina, N Paraguay and E Brazil.

S. h. albomarginata Spix, 1824 - SE Brazil, E Paraguay and NE Argentina (Misiones).



Descriptive notes. c. 34 cm. Facial disc blackish, eyebrows and margins of disc speckled white; entire body blackish-brown, upperparts with very narrow and wavy white bars, underparts with very regular bars that widen slightly downwards; tail black with c. 4 narrow white bars and broader white tip; tarsus feathered, barred; iris orange to brown, possibly related to age; bill and toes orange-yellow. Differs from *S. nigrolineata* in barred crown and upperparts. Juvenile browner, heavily barred. Race *albomarginata* tends to be darker, blacker, with white barring more prominent. Voice. Typical song an ascending series of 4 deep and low-pitched "bht"

notes, followed by a sharp and slightly descending "bUhu" note after a longer pause of c. 1-5 seconds; sometimes sounds very like *S. nigrolineata*, and the two will respond to one another's calls.

Habitat. Humid forest and clearings; also in *Araucaria* forest in S of range. In some areas has adapted to man-made habitats, occasionally found in coffee and banana plantations. From sea-level to 200 m, often to 500 m, rarely reported to 1400 m.

Food and Feeding. Primarily insects, especially beetles, locusts and mantids; some small vertebrates. Nocturnal; forages in canopy.

Breeding. No information.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Appears to be scarce throughout entire range; no quantitative figures available. Nominate *huhula* was found to be locally not uncommon in mid 1950's, e.g. in N Argentina, but has declined since then. Occurs in several protected areas throughout its range, such as Amacayacu National Park (Colombia), Imataca Forest Reserve (Venezuela) and Manu National Park (Peru). Because it is essentially a forest owl, species is susceptible to habitat destruction by the transformation of rainforest into monocultures and ranchland. Conservation status perhaps merits re-evaluation.

Bibliography. Boesman (1998), Brooks, Barnes *et al.* (1993), Brooks, Clay *et al.* (1995), Canevari *et al.* (1991), Chebez (1994), Cohn-Haft *et al.* (1997), Eriksen & Amarilla (1997), Fjeldså & Mayer (1996), Haverschmidt & Mees (1994), Hayes (1995), Hilty & Brown (1986), Kirwan & Sharpe (1999), Lowen, Clay, Barnett *et al.* (1997), Lowen, Clay, Brooks *et al.* (1995), Meyer de Schauensee & Phelps (1978), Olrog (1985), Partridge (1956), de la Peña (1994), do Rosário (1996), Short (1975), Sick (1993, 1997), Snyder (1966), Stotz *et al.* (1996), Tostain *et al.* (1992).

112. Rufous-banded Owl

Strix albitarsis

French: Chouette fasciée **German:** Rötelskauz **Spanish:** Cárabo Patiblanco

Taxonomy. *Syrnium albitarse* Bonaparte, 1850, Bogotá.

This species, along with *S. virgata*, *S. nigrolineata*, *S. huhula* and sometimes Afrotropical *S. woodfordii*, often placed in separate genus *Ciccaba* on basis of differences in external ear structure compared with *Strix*, but DNA studies show that generic separation not warranted. Affinities uncertain; seems not to be closely related to other Neotropical *Strix*. Bolivian population sometimes separated as *tertia*. Species name often incorrectly spelled *albitarsus*. Monotypic.

Distribution. Andes from N Venezuela S to W & C Bolivia.



Descriptive notes. 30-36 cm. Mid-sized owl with rounded head and distinctive plumage pattern. Facial disc rufous, becoming blacker around eyes, with prominent buffy-white eyebrows and lores, black chin; rest of head and upperparts blackish-brown, barred and spotted buffy-rufous; flight-feathers and tail barred, primaries notched with rufous on outer web; throat white; chest dark brown, barred and spotted tawny and whitish, forming broad but rather diffuse chest band; rest of underparts with feathers edged silvery-white and with rufous-brown central area, producing large, squarish white spots that give ocellated appearance; tarsus feathered whitish;

iris orange-yellow; bill pale yellow; toes whitish to creamy. Juvenile uniformly buff, with blackish mask, brown eyes. Voice. Fast series of short, deep, deliberate notes, "hu, hu-hu-hu, HOOa", with pause after first note, next 3 quicker, and final note protracted and strongly emphasized, rhythm thus different from those of *S. huhula* and *S. nigrolineata*; repeated at intervals of 8-11 seconds.

Habitat. Humid montane evergreen forest and cloudforest, from c. 1700 m to 3700 m; in Venezuela, found in open areas with scattered trees between forested parts.

Food and Feeding. Diet uncertain; probably insects and small mammals. Nocturnal; also active shortly after dark and before dawn. Forages in canopy.

Breeding. Recently fledged bird found in third week Jun in Colombia; juvenile seen in Aug in Venezuela; no other information.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Status uncertain; locally fairly common, but few reliable data. Has been recently recorded along the Mérida-La Azulita road and Páramo de Tamá (Venezuela), near Rio Blanco (Colombia), at Paschoa Forest Reserve and along the Nonomindo and Baeza-Tena roads (Ecuador). Probably adversely affected by cutting of forest habitat. Further study needed.

Bibliography. Baez *et al.* (1997), Fjeldså & Krabbe (1990), Fjeldså & Mayer (1996), Hilty & Brown (1986), Krabbe *et al.* (1997), Meyer de Schauensee & Phelps (1978), Olrog (1968), Ridgely & Gaulin (1980), Stotz *et al.* (1996), Vélez & Velázquez (1998).

Genus *JUBULA* Bates, 1929

113. Maned Owl

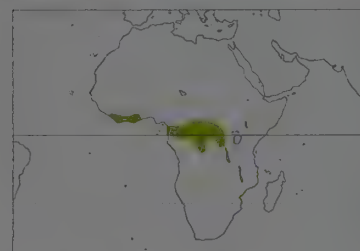
Jubula lettii

French: Duc à crinière

German: Mähneule

Spanish: Búho de Crin

Other common names: Akun Scops-owl

Taxonomy. *Bubo letti* Büttikofer, 1889, Passy District, Liberia.Affinities uncertain. Sometimes suggested that genus be merged with Neotropical *Lophotrix*; superficial similarities in appearance and similar ecology, however, probably due to convergent evolution. Monotypic.**Distribution.** Liberia, Ivory Coast and Ghana; and patchily from S Cameroon and N Gabon to E Zaire.**Descriptive notes.** c. 40 cm; 1 female 183 g. Highly distinctive. Elongated crown and nape feathers forming brown and white "mane", merging with bushy brown-and-white ear-tufts; rufous facial disc edged in brown, with contrasting white forehead, eyebrows and lores; mantle and back chestnut, scapulars with black-edged whitish outer webs; wing-coverts brown-rufous with creamy and dark vermiculations; flight-feathers and tail barred rufous and buff; throat white; upper breast light rufous, fading to buff or whitish on belly, with dusky brown streaks; tarsus feathered; iris yellow to orange-yellow; bill pale yellow; toesyellow. Sexes similar, female darker and more heavily patterned. Juvenile head and neck almost white, rest washed buff with faint rufous bars. Voice. Reported as mellow "who", followed after 10-12 seconds by similar but higher-pitched note; this vocalization, however, unconfirmed for present species, possibly made by *Scotopelia bouvieri*.**Habitat.** Lowland rainforest and gallery forest, especially with abundant creepers; reportedly associated with old forest, but little known. Often roosts in creepers.**Food and Feeding.** Little information. Insects such as grasshoppers and beetles possibly most important; green vegetable matter found in stomach of young bird. Small, weak feet and bill suggest incapability of capturing larger vertebrate prey; although birds not known to be taken, frequently mobbed by passerines. Strictly nocturnal; emerges at dusk.**Breeding.** Pair with full-grown young observed at Mt Nimba, in Liberia, in third week Feb; observations in Zaire suggest laying during Mar-May; fledglings seen in late Dec and Jan in Cameroon and Gabon. No other details known.**Movements.** Resident; presumed sedentary.**Status and Conservation.** Not globally threatened. CITES II. Very poorly known; status difficult to assess owing to species' secretive and nocturnal habits, and because of scant information on its biology. Reported as very scarce in Ghana, and rare in Liberia, but probably mainly overlooked; only few Cameroon records; no meaningful data from rest of range. Density estimated at 1 pair/1-1.5 km² of forest, so possibly more common than records suggest. Never recorded outside forest or forest clearings; possibly at some risk from habitat loss through harvesting of timber.**Bibliography.** Bannerman (1953), Brosset & Énard (1986), Christy & Clarke (1994), Clark & Mikkola (1989), Colston & Curry-Lindahl (1986), Dowsett & Dowsett-Lemaire (1991, 1993), Dowsett & Forbes-Watson (1993), Dowsett *et al.* (1999), Dowsett-Lemaire (1992, 1996), Fry *et al.* (1988), Gatter (1988, 1997), Grimes (1987), Kemp & Kemp (1998), Lippens & Wille (1976), Louette (1981), Mackworth-Praed & Grant (1970), Snow (1978), Stephenson & Newby (1997), Thiollay (1985).Genus *LOPHOSTRIX* Lesson, 1836

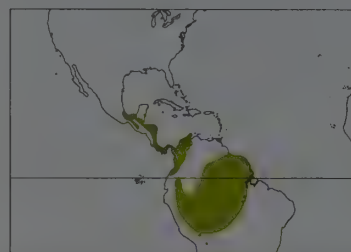
114. Crested Owl

Lophotrix cristata

French: Duc à aigrettes

German: Haubenkauz

Spanish: Búho Corniblanco

Taxonomy. *Strix cristata* Daudin, 1800, French Guiana.Genus considered by some to be related to *Otus*, and by others to *Bubo*. Recent studies, however, also suggest that it may have some link with *Pulsatrix*. Superficial resemblance to Afrotropical *Jubula* considered probably due to convergence. Race *stricklandi* possibly specifically distinct. Three subspecies recognized.**Subspecies and Distribution.***L. c. stricklandi* P. L. Sclater & Salvin, 1859 - S Mexico to W Panama and W Colombia.*L. c. wedeli* Griscom, 1932 - E Panama to NE Colombia and NW Venezuela; possibly also N Venezuela (1 specimen from Aragua).*L. c. cristata* (Daudin, 1800) - S Venezuela and the Guianas to N Brazil (W Pará), S through Amazonia to N Bolivia and N Mato Grosso, then W to SW Colombia, E Ecuador and E Peru.**Descriptive notes.** 36-43 cm; 400-600 g. Highly distinctive; polymorphic. Pale morph with facial disc tawny to chestnut, white eyebrows continuing into very long, mostly white ear-tufts; upperparts rather plain buffy-brown to grey-brown, wing-coverts spotted with white; off-white below, darker on breast; tarsus feathered; iris dark brown; bill pale yellow; toes greyish to yellow. Dark morph dark brown above, pale brown below, facial disc dark rufous with blackish border. Juvenile with short ear-tufts, dark facial disc, white body plumage, mixed pattern on wing-coverts. Race *stricklandi* distinct, with blackish face and forehead, dark rufous around eyes, white-edged scapulars; eyes usually yellow-orange. Voice. Deep, emphatic growl, "k.k.k'k'k'kkrrrrr", repeated every c. 9 seconds. Race *stricklandi* shorter "gurr" or "kwarr" at irregular intervals.**Habitat.** Humid forest, tall second growth, gallery woodland and heavy forest; roosts by day in dense vegetation, often low down. Sea-level to 1900 m; reported from cloudforest at 1950 m in Honduras; to 1200 m in Guatemala.**Food and Feeding.** Primarily large insects (beetles, orthopterans, caterpillars); probably some small vertebrates. Strictly nocturnal. Little known of foraging behaviour; perches in gaps and at edges, and along streams.**Breeding.** Lays Feb-May, in dry to early wet season. Nest in tree hole; report of nesting in loft of house. Young thought possibly to accompany parents at least through Sept.**Movements.** Resident.**Status and Conservation.** Not globally threatened. CITES II. Very poorly known, and no reliable quantitative data on population level; considered uncommon to fairly common in

Mexico; rare to fairly common in Costa Rica; rare in Panama and Colombia. Has been recently recorded at Lagos de Montebello and Palenque, Chiapas (Mexico), along the Pipeline road (Panama), at Caura and Imataca Forest Reserve, Bolívar (Venezuela), and near Iquitos (Peru). Information required on population size, ecology and behaviour. Habitat loss and deforestation a likely threat to species, which needs at least patchy forest.

Bibliography. Binford (1989), Bousman (1998), Haverschmidt & Mees (1994), Hilty & Brown (1986), Howell & Webb (1995a), Kirwan & Sharpe (1999), Land (1970), Lentino *et al.* (1984), Meyer de Schauensee & Phelps (1978), Monroe (1968), Orians & Paulson (1969), Ridgely & Gwynne (1989), Sick (1993, 1997), Slud (1960, 1964), Snyder (1966), Stiles & Skutch (1989), Storer (1972), Stotz *et al.* (1996), Thurber *et al.* (1987), Tostain *et al.* (1992), Wetmore (1968a).Genus *PULSATRIX* Kaup, 1848

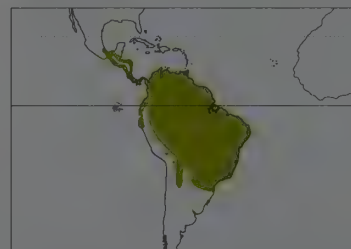
115. Spectacled Owl

Pulsatrix perspicillata

French: Chouette à lunettes

German: Brillenkauz

Spanish: Lechuzón de Anteojos

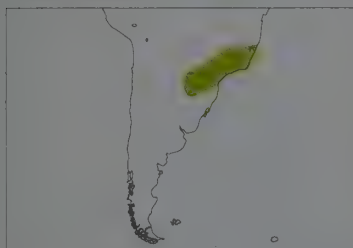
Taxonomy. *Strix perspicillata* Latham, 1790, Cayenne.Races *chapmani*, *trinitatis* and *boliviana* poorly differentiated, perhaps not valid. Six subspecies recognized.**Subspecies and Distribution.***P. p. saturata* Ridgway, 1914 - S Mexico (Veracruz and Oaxaca) to W Panama (Pacific Slope to Chiriquí).*P. p. chapmani* Griscom, 1932 - Caribbean slope of Costa Rica through E Panama to Colombia, W Ecuador and NW Peru.*P. p. trinitatis* Bangs & Penard, 1918 - Trinidad.*P. p. perspicillata* (Latham, 1790) - Venezuela, the Guianas, Brazil, and from E Colombia S to N Bolivia.*P. p. boliviana* L. Kelso, 1933 - S Bolivia and N Argentina.*P. p. perspicillata* (Wied, 1820) - E Brazil (Bahia S to Rio Grande do Sul) and Paraguay, probably also NE Argentina (Misiones).**Descriptive notes.** 43-52 cm; 590-980 g. 1050-1250 g (*pulsatrix*). Large owl. Facial disc very dark brown, with prominent white eyebrows and lores; head and neck blackish-brown, rest of upperparts paler, dark brown, flight-feathers and tail barred grey-brown; throat white; underparts pale buff, with broad chocolate-brown breast-band; tarsus and toes feathered; iris bright yellow; bill creamy-yellow. Juvenile with facial disc blackish, body completely white, wing-coverts barred grey-brown; several plumage stages before whiteness lost, can take up to 5 years to reach adult plumage. Race *saturata* darker, more sooty-black on head and mantle, finely barred below; *pulsatrix* with head and back uniform brown, chest band broken in centre, eyes more orange or brownish-yellow. Voice. Deep, descending sequence, "PUP-pup-pup-po" or "PUM-PUM-pum-pum", acceleration; female slightly higher, often duets; race *pulsatrix* slower, without acceleration; juvenile a loud whistle and gruff "juuiiu".**Habitat.** Dense tropical rainforest and edges, savanna woodland and dry forest; also areas with scattered trees, coffee plantations and gallery-forested streams; occasionally to 1500 m. Perches alone or in pairs; often along streams in gallery forest.**Food and Feeding.** Primarily vertebrates: small mammals up to size of opossums (Didelphidae), rabbits (Leporidae), skunks (Mustelidae), and rodents such as *Oryzomys bicolor* and agoutis (*Dasyprocta*, *Myoprocta*); sometimes bats, frogs, small reptiles such as lizards, and birds such as doves (Columbidae), motmots (Motmotidae), jays (Corvidae) and oropendolas (*Psarocolius*); also insects such as grasshoppers, large scarab beetles (Scarabaeidae) and large caterpillars, and small crustaceans such as crabs. Nocturnal. Hunts from perch, taking prey from ground or foliage.**Breeding.** Lays mostly Apr-Jun, in dry season and early wet season; some variation, e.g. Sept-Oct in Panama, Aug in Surinam; young observed in Sept in Costa Rica. Nest in large tree cavity. 2 eggs, rarely 3; incubation by female, c. 5 weeks; usually only 1 chick survives, brooded by female, leaves nest at 5-6 weeks, remains with parents for up to 1 year after fledging.**Movements.** Resident.**Status and Conservation.** Not globally threatened. CITES II. Very local, but often considered fairly common where it occurs. Fairly common to uncommon in Mexico; locally from rare to common (Palo Verde and Santa Rosa National Parks) in Costa Rica; fairly common locally in Colombia. Occurs in a considerable number of protected areas throughout its extensive range. Localized distribution due to forest destruction; needs at least patchy forest for nesting and roosting; habits much as *Lophotrix cristata*, but more tolerant of deforestation than latter. Little information regarding abundance, population ecology or behaviour.**Bibliography.** Belton (1984), Binford (1989), van Bockstaele (1977), Bohmke & Macek (1994), Canevari *et al.* (1991), Contreras *et al.* (1990), Fjeldså & Mayer (1996), Gómez de Silva *et al.* (1997), Haffer (1975),

Haverschmidt & Mees (1994), Hayes (1995), Herklots (1961), Hilty & Brown (1986), Howell & Webb (1995a), Land (1970), Lowery & Dalquest (1951), Meyer de Schauensee & Phelps (1978), Monroe (1968), Olrog (1985), de la Peña (1994), Ridgely & Gwynne (1989), do Rosário (1996), Short (1975), Sick (1993, 1997), Slud (1964), Snyder (1966), Stiles & Skutch (1989), Stotz *et al.* (1996), Thurber *et al.* (1987), Tostain *et al.* (1992), Wetmore (1968a).

116. Tawny-browed Owl *Pulsatrix koeniswaldiana*

French: Chouette à sourcils jaunes **Spanish:** Lechuzón Acollarado Chico
German: Gelbbrauenkauz
Other common names: White-chinned Owl

Taxonomy. *Syrnium Koeniswaldianum* M. Bertoni and W. Bertoni, 1901, probably from near Puerto Bertoni on the Alto Paraná, Paraguay. Possibly forms superspecies with *P. melanota*. Sometimes treated as conspecific with latter, but morphology and vocalizations differ. Monotypic.
Distribution. E Paraguay, extreme NE Argentina (Misiones), and S Brazil (from Espírito Santo S to Santa Catarina).



Descriptive notes. c. 44 cm. Facial disc brown, encircled by ochre, with white rictal bristles near bill, small white chin patch and creamy eyebrows; uniform dark chocolate-brown above, flight-feathers faintly barred with whitish, tail more prominently barred white; breast dark brown, forming broad, distinct band; belly buff; rest of underparts light ochre, often with slight hint of vermiculations; tarsus feathered; iris brownish; bill yellow-horn; toes greyish. Differs from *P. perspicillata* in ochre and creamy (not white) "spectacles" and facial rim, and smaller size; from *P. melanota* in lack of obvious barring on breast and belly. Juvenile

similar to *P. perspicillata*, but eyes dark, face brown rather than black. **VOICE.** Low, descending sequence of ventriloquial "brrr brrr brrr brrr" or "ut ut ut ut" notes, accelerating and weaker at end; female responds with higher-pitched call.

Habitat. Humid, tropical forest and more open woodland; also *Araucaria*-dominated forest; in S Misiones, Argentina, recorded in degraded and marginal forest. From sea-level to 1500 m.

Food and Feeding. Small mammals, birds and large insects; probably also other small vertebrates. Nocturnal; forages in canopy; hunts from perch.

Breeding. Season uncertain. Nest in tree hole, usually 2 eggs; incubation c. 5 weeks, by female; nestling with white down and dark facial disc; young leave nest at 5-6 weeks, unable to fly; cared for by parents for some months further.

Movements. Probably resident.

Status and Conservation. Not globally threatened, CITES II. Restricted-range species; present in Atlantic Forest Lowlands EBA. Considered relatively rare, or at best uncommon; probably overlooked. Has apparently decreased in Argentina owing to timber-cutting in Misiones, although still regularly recorded and possibly locally not uncommon. In Brazil, occurs in several protected areas,

such as Sooretama Biological Reserve and Itatiaia National Park. Suffers some road casualties. Species should be monitored simply because of scale of habitat loss in its range, and because it is too poorly known to speculate on its true status.

Bibliography. Brooks *et al.* (1993), Canevari *et al.* (1991), Chebez (1994), Hayes (1995), Lowen, Clay *et al.* (1997), Olrog (1968, 1984, 1985), de la Peña (1994), Pereyra (1950), do Rosário (1996), Saibene *et al.* (1996), Schubart *et al.* (1965), Sick (1993, 1997), Stattersfield *et al.* (1998), Stotz *et al.* (1996).

117. Band-bellied Owl *Pulsatrix melanota*

French: Chouette à collier **German:** Bindenkauz **Spanish:** Lechuzón Acollarado Grande
Other common names: Rusty-barred Owl(!)

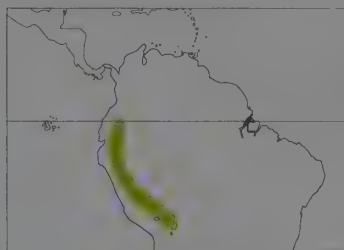
Taxonomy. *Noctua melanota* Tschudi, 1844, Peru.

Possibly forms superspecies with *P. koeniswaldiana*. Sometimes considered to include latter as race, but morphology and vocalizations differ. Validity of race *philoscia* uncertain. Two subspecies recognized.

Subspecies and Distribution.

P. m. melanota (Tschudi, 1844) - possibly SE Colombia; E Ecuador, and N Peru to SE Peru.

P. m. philoscia Todd, 1947 - WC Bolivia.



Descriptive notes. c. 48 cm. Facial disc brown, with conspicuous white eyebrows and lores; head otherwise uniform dark brown; upperparts chocolate-brown with few buffy-white spots; flight-feathers and tail with widely spaced, thin white bars; throat brown, with distinct white collar below; upper breast rufous-brown, barred and mottled with buff; rest of underparts white, barred reddish-brown, fading to scattered brown bars on creamy belly; tarsus feathered; iris dark red-brown; bill pale, creamy-yellow; toes light greyish. Distinguished from *P. perspicillata* and *P. koeniswaldiana* in clearly barred underparts. Juvenile undescribed. Race

philoscia possibly larger. **VOICE.** Short, deep trill followed by very fast series of 4-5 popping sounds; several deep, muffled hoots recorded in Peru.

Habitat. Humid tropical rainforest; perhaps also more open woodland locally. Found from lowlands to c. 1600 m, mainly above 700 m.

Food and Feeding. Poorly known. Nocturnal.

Breeding. No information.

Movements. Probably resident.

Status and Conservation. Not globally threatened, CITES II. Very poorly known; considered relatively rare, and very few reliable records, although apparent rarity possibly due partly to species' nocturnal habits and seldom penetrated forest habitats. Has been recently recorded at Coca Falls and along the Loreto road, Ecuador. Single specimen possibly from Colombia, but lacks locality and date. In general, species could be threatened by habitat loss.

Bibliography. Balchin & Toynne (1998), Butler (1979), Hilty & Brown (1986), Meyer de Schauensee (1982), Olrog (1968), Parker *et al.* (1982), Stotz *et al.* (1996), Taylor (1995), Traylor (1958a), Williams *et al.* (1996).

PLATE 14



118

ssp caparoch



ssp ulula



119



with head turned



rufous morph

120

grey-brown morph



ssp licua

121



ssp perlatum



grey morph

122

rufous morph



123



brown morph

124



rufous morph



125

Subfamily SURNIINAE

Tribe SURNIINI

Genus *SURNIA* Duméril, 1806

118. Northern Hawk-owl

Surnia ulula

French: Chouette épervière

German: Spereule

Spanish: Cárabo Gavilán

Other common names: Hawk Owl

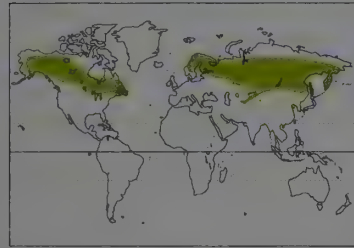
Taxonomy. *Strix Ulula* Linnaeus, 1758, Sweden.

Relationships uncertain; placed near *Glaucidium*, which with *Xenoglaux*, *Microathene* and *Athene* comprise tribe Surniini, on basis of osteology and DNA. Siberian populations, formerly separated as *pallasi*, included in nominate. Three subspecies recognized.

Subspecies and Distribution.

S. u. ulula (Linnaeus, 1758) - N Eurasia E to Kamchatka and Sakhalin, C Siberia S to Tarbagatay. *S. u. tianschanica* Smallbones, 1906 - C Asia and NW & NE China, possibly also N Mongolia.

S. u. caparoch (P. L. S. Müller, 1776) - Alaska through Canada to Newfoundland, S to extreme N USA.



Descriptive notes. 36-39 cm; wingspan 74-81 cm; male 270-314 g, female 320-345 g. Distinctive owl with long tail, broad head, thick-set body, and blackish, dark brown and white plumage pattern; flight and perching hawk-like, flight straight and unhurried, combining bursts of wingbeats with glides. Facial disc greyish-white, with almost black line from eye dividing at hindcrown to create black band around disc and another down nape side; black band may join with dull black-brown bars across upper breast and almost black chin to complete bold dark outline to face, posing strong contrast to relatively faintly barred white breast;

crown black-brown, thickly spotted white, sides of crown almost fully white; nape black-brown, with few white spots and lateral dusky patches opposing lower nape; mantle and back mostly dark brown; white spots on scapulars, appear as pale panels when wing folded; rump and tail black-brown with dull white bars, most obvious on spread tail; white below, closely and heavily barred black-brown; eyes yellow; bill yellow-horn; legs and toes fully feathered and white. Juvenile upperparts grey-brown (less blackish), less extensively marked white. North American race *caparoch* blacker above, tawny below, particularly on flanks and lower belly; slightly larger *tianschanica* even blacker above, with smaller white marks, somewhat intermediate below. **VOICE.** Male gives rapid, trilling "prullul-lullul" with burbling quality, lasting up to 14 seconds; corresponding call of female shriller, shorter and less sonorous; also harsh chattering "ke-ke-ke-ki" and other short, sharp and trilled calls.

Habitat. Occupies forest tundra and boreal taiga as far as tree-line and ranging S to edge of forest steppe and cultivated land. Seeks ready access to clearings, burnt areas, open peatland or muskeg, dry eminences or ridges, and sparse woodland, including birch, aspen and mixed woods, with some preference for pine (*Pinus*), larch (*Larix*) and stunted *krummholz* trees, especially if terminating in broken-topped stumps or bare branches; avoids dense coniferous forest. In winter in North America, inhabits open heathland and prairies, even perching on haystacks.

Food and Feeding. In breeding season, almost wholly small voles (*Microtinae*), with few small birds and larger mammals; also occasional amphibian, fish or insect. Cannibalism known to occur, adults eating own young. Mammals include but are not limited to voles (*Clethrionomys*, *Arvicola*, *Microtus*); birds up to size of thrushes (*Turdus*), but recorded up to size of Willow Grouse (*Lagopus lagopus*). May eat more birds in winter (up to 90% in Fennoscandia), perhaps taking fewer voles because of lower numbers and snow cover. North American race *caparoch* found to prey on juvenile snowshoe hares (*Lepus americanus*); for owls to breed successfully, hares contributed 40-50% of prey biomass during peak years of hare cycle; in general, hares, as well as squirrels (*Tamiasciurus*, *Spermophilus*), may be critical prey items when vole populations low. In China, diet mainly rats. Diurnal and nocturnal. Hunts from exposed perch; changes from one habitual perch to next; pounces on prey or skims down over ground; hovers frequently; can seize prey in flight; sometimes plunges into snow, hunting by sound.

Breeding. Season c. Mar-Sept. Presumably seasonally monogamous; occasional polygyny; no data available on possible incidence of monogamy persisting more than 1 breeding season. Nest in cavity, hole in trees, top of stumps, or nestbox, occasionally old nest of raptors or crow; no fresh material brought to nest. 6-10 eggs, clutch size sometimes increasing to 8-13 in good vole years; eggs laid at intervals of 1-2 days; 1 brood, with replacements laid after egg loss; female incubates and broods, male brings food to nest and sometimes covers eggs when female away; incubation 25-30 days; young altricial, scramble out on to nearby branches before capable of flight, fledge at 25-35 days; young remain in territory 6-8 weeks, cared for by both parents, which sometimes perform distraction-lure display of disablement type when intruder approaches, flying off with "sree" call, landing on ground or stump, drooping wings, and fluttering and calling on ground for several minutes; young independent at c. 75 days. In Canada, fledging success complete for 8 of 9 broods observed. Sexual maturity at 1 year.

Movements. Dispersive and irruptive; essentially nomadic; dependent largely on prey availability. When voles at normal levels, birds breed and winter in N; when vole numbers crash (usually every 4 years), irruptions occur, many individuals dispersing S, mostly juveniles; also, ringed birds have been recovered both NE and SE of ringing locality, at distances of up to 1860 km. Winters irregularly S to N USA, Kuril Is and C & SE Europe; vagrants of nominate race recorded in British Is and S to Yugoslavia and Romania; vagrants of race *caparoch* to Bermuda, Britain and Canary Is.

Status and Conservation. Not globally threatened. CITES II. Numbers fluctuate markedly with abundance of small rodents. Difficult to assess population status or trends; breeding range far removed from most human population centres; almost impossible to census visually in breeding areas. In Europe, believed to have declined markedly, since more recent periodic invasions in S have been on fairly small scale compared with earlier ones. Even in good vole years, nests are usually several kilometres apart; in Norway, population estimated at 1000-10,000 breeding pairs in mid 1990's, with 1 pair/50 km² typical; in Sweden, population estimated half that of Norway, but in exceptional rodent years (e.g. 1976) up to 10,000 pairs and density may increase locally to 1 pair/5 km². In Finland, population has declined since 19th century, as a result of disappearance of hollow trees and through human persecution; tentative estimate c. 3600 pairs, with marked annual fluctuations from almost absent to fairly common, and with some evidence of recovery since 1960's. In Russia, common in N taiga, numbers fluctuating with rodent populations. Rare in China. In North America, populations likely to have been stable over past 10-100+ years, but trends impossible to quantify owing to remote breeding range, low breeding densities, and erratic distribution and numbers during winter irruptions in inhabited areas. Diurnal habits and lack of fear of humans increase vulnerability. Also in North America, while more than 50% of breeding range is in N forests that are currently non-commercial, forestry activities in that region have expanded since c. 1970. Modification of clear-fell logging practices could enhance habitat; cuts of less than 100 ha, interspersed with forest patches and staggered over time, probably optimal; inclusion of suitable numbers of stumps, snags and trees for perching and nesting would provide year-round habitat. Also, fire suppression reduces availability of suitable nest-sites; population known to hunt and nest in old burnt areas.

Bibliography. Armstrong (1983), Axelrod (1980), Baekken *et al.* (1987), Baieich & Harrison (1997), Beaman & Madge (1998), van den Berg (1984), Byrkjedal & Langhelle (1986), Campbell *et al.* (1990), Cramp (1985), Crowell (1982), Duncan (1990), Duncan & Duncan (1998), Duncan & Harris (1997), Eckert, A.W. (1974), Eckert, K.R. (1997), Échécopar & Hue (1978), Fisher (1974), Flint *et al.* (1984), Forsman (1980, 1996, 1998), Fragner (1995d), Fridén (1984), Haas (1991), Hagemeijer & Blair (1997), Hagen (1956), Heintzelman (1992), Hogstad (1986), Huhtala *et al.* (1987), Ims (1982), James, P.C. (1995), James, R.D. & Nash (1983), Jensen (1988), Johnsgard (1988), Jones (1987a), Kaufman (1996), Kehoe (1982), Kertell (1986), Korpiakäi (1992a), Lane & Duncan (1987), Lang *et al.* (1991), Markgren (1985), McNair (1994), Mikkola (1970/71, 1983), Nybo & Sonerud (1990), Persson (1986), Pleshak (1987), Portenko (1973), Robiller (1982), Rogacheva (1992), Rogge (1973), Rohner *et al.* (1995d), Root (1988), Seutin (1990), Simeonov *et al.* (1990), Simon & Simon (1980), Snow & Perrins (1998), Sonerud (1985, 1992b, 1997), Sonerud *et al.* (1987), Stepanyan (1990), Tyler & Phillips (1978), Voous (1988), Walker (1993), Wilson (1993), Wolfe & de la Torre (1990), Zhao Zhengjie (1995).

Genus *GLAUCIDIUM* Boie, 1826

119. Eurasian Pygmy-owl

Glaucidium passerinum

French: Chevêche d'Europe

German: Sperlingskauz

Spanish: Mochuelo Alpino

Other common names: Pygmy Owl/Owlet, Northern Pygmy-owl(!), Old World Pygmy-owl: European Pygmy-owl (*passerinum*)

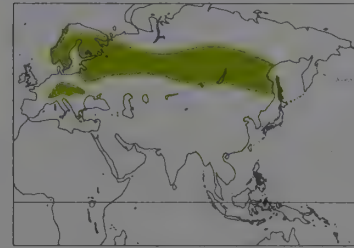
Taxonomy. *Strix passerina* Linnaeus, 1758, Sweden.

Sometimes considered to form superspecies with *G. brodiei*, *G. perlatum*, *G. californicum* and *G. gnoma* (including recently separated *G. cobanense* and *G. hoskinsii*), but DNA evidence clearly shows that present species and *G. californicum* are not closely related. Race *orientale* intergrades with nominate in W Siberia and Altai Mts. Two subspecies recognized.

Subspecies and Distribution.

G. p. passerinum (Linnaeus, 1758) - from Scandinavia and mountains of S, C & E Europe E across NW & C Russia and Siberia to Sakhalin and NE China.

G. p. orientale Taczanowski, 1891 - C & E Siberia.



Descriptive notes. 16-17 cm; wingspan 34-36 cm; male c. 50-65 g, female c. 67-77 g. Tiny, small-headed owl with flight bounding and dashing. Dimorphic, with brown and grey morphs and varying sharpness of marks: brown morph predominant in most of range, grey predominant only in C & E Siberia. Facial disc dusky with short, almost white eye-brows; bill dull white; indistinct grey-white half-circles on outer cheeks; eyes small and yellow, appearing close-set; upperparts dark dull brown, spotted white-buff overall; flight-feathers dark brown, narrowly barred white-buff; tail dark brown with narrow but distinct buff-white barring; underparts mostly white, upper breast and sides of chest barred dark brown; underwing-coverts noticeably white, contrasting with dark, faintly barred flight-feathers; legs and toes feathered white. When true size not evident, can be confused with *Aegolius funereus*, but distinguished by small head, lack of scapular spotting, and sharp white bars on rather long and square-cut tail; differs from dark races of *Athene noctua* in lack of bold white spots on scapulars, less white-buff spotting, narrower and relatively longer white-barred tail, and longer bill. Juvenile darker, with dusky brown, unspotted upperparts and wing-coverts, unbarred patches on chest sides, thinner streaks on pale underparts. Siberian race *orientale* has paler upperparts which show purer white and more sharply defined spots; breast and flanks more strongly marked brown.

VOICE. Flute-like "deu", repeated monotonously 5-10 times per 10 seconds; bouts of calling may last several minutes.

Habitat. Open coniferous and mixed forest: found in taiga and montane forest, mainly coniferous, sometimes to tree-line; commonly in forest of silver fir (*Abies alba*). In lowlands at upper and middle latitudes; in temperate zone ranging from 250-300 m in narrow cool and moist ravines to above 1000 m in Alps (highest 2150 m). Overall, mainly in tall forest interior, dominated by conifers and often interspersed with beech (*Fagus*), aspen (*Populus*), birch (*Betula*) and other broadleaved

trees used for nesting. Needs access to clearings, moors, meadows or avalanche pathways. Roosts largely in cover of foliage or by tree trunks.

Food and Feeding. Small mammals, especially voles (*Microtinae*), and small birds. In S Finland, during breeding season, voles comprised 58.7% of diet and birds 39.5%. Mammals also include e.g. shrews (*Sorex*), bats (*Myotis*) and mice (*Micromys*, *Apodemus*). Bird prey rarely larger than finches (*Fringillidae*), but occasionally up to size of full-grown woodpeckers (*Dendrocopos*) and thrushes (*Turdus*). In S Finland, towards end of breeding season, diversity of bird prey and proportion in diet increased, apparently because of reduced availability of small mammals (due to growth of vegetation) and increased availability of birds, especially fledglings: in first half of nestling period, young birds made up 18%, in second half 31%. Primarily crepuscular, occasionally diurnal. Prey located by sight; night vision poor. Relies on surprise; hunts mammals from open perch, dropping or gliding on to prey; hunts birds from concealed perch, snatching from branches or striking from below, and will hunt at birdtables. Strikes small mammals with feet and bites them on snout; birds apparently killed with feet and/or bites to head or neck. Prey carried in foot to concealed place for eating; items for delivery to nest or cache often first decapitated. Birds plucked; all prey eaten piecemeal, intestines rejected. Summer caches are small (1 item) and usually on branches or other open sites; in N Europe, caching peaks in Nov-Jan (200 items recorded) and usually in holes, occasionally nestboxes; large caches made only in years with dry and cold Nov and early Dec; apparently no link with prey availability.

Breeding. Season Apr-Jul. Monogamous; pair-bond lasts 1 season, though sometimes renewed after temporary severance in late autumn; pair-bonding involves alternating fear of and aggression towards mate, with pursuit and attacks occurring. Nest in tree cavity, either natural hole or one excavated by woodpecker; will make use of nestboxes; no material added, but debris may be removed; nest-showing begins 6-8 weeks before laying. 4-7 eggs; replacement clutch probably laid after egg loss; female incubates, broods and feeds young in nest, male hunts during incubation and most of nestling phase; female sometimes stimulates male to hunt by apparent attacks; incubation 28-30 days, beginning with last egg; hatching synchronous; fledging 27-34 days; young fed by parents for c. 4 weeks after fledging, at which point parents drive them out of territory. In W Germany, 57 young fledged from 17 nests, averaging 3.3 per nest; in SE Norway, average number of fledged young per egg 0.52-0.94, result of variations in clutch size (5.8-7.3) and food supply. Age of first breeding 1 year.

Movements. Mainly resident. In winter, may shift to broadleaved mixed woodland with some conifers or to neighbourhood of human settlements, with degree of dispersal higher in N than in C Europe. Irregularly irruptive in N Europe; probably triggered by combination of cold weather and rodent scarcity.

Status and Conservation. Not globally threatened. CITES II. In Fenno-Scandia, breeding densities and numbers fluctuate markedly with weather conditions and rodent cycles: in mid 1990's, estimated number of breeding pairs in Norway 2000-6000, in Sweden 10,000-20,000 and in Finland 5000-7000; highest densities up to 30 pairs/10 km² but varying locally over 100-fold. Finnish estimate of 200-300 pairs in 1958 undoubtedly too low; no evidence of decline in Finland, despite large-scale destruction of old forest. Population fluctuates much less in mountains of C Europe, where probably 4100-7200 breeding pairs with density generally 0.7-4.2 pairs/km². In W Germany, has disappeared from large parts of range, linked to deforestation and resulting changes in ecosystem, such as increase in population of *Strix aluco* at higher elevations. In Black Forest, extinct by 1967; captive-breeding programme begun in 1968, and 150 breeding territories in whole of Black Forest by 1995; in this reintroduction, birds used artificial nests only once, and woodpecker cavities very important for species. E German population fluctuates, probably 120-150 pairs (1980). In E Poland (Białowieża Forest) and Belarus, 1300-2600 breeding pairs; in Austria c. 2000 pairs, with fewer in SE France, Switzerland, N Italy, Slovenia, Czech Republic (some recent increase in S Bohemia), Slovakia, Romania and Ukraine. Small isolated population in Rodopi Mts of Bulgaria, and in 1986 species first found nesting in Greece at 1230 m above sea-level in Vardhousia Óri Mts. Probably over 1000 pairs in Baltic states (Estonia and Latvia), but greatly decreased by mid 1960's in Lithuania and now very rare. Russian population estimated at 10,000-100,000 pairs.

Bibliography. Augst (1990, 1992), Augst & Manka (1997), Axer (1977), Barruel (1950), Beaman & Madge (1998), Bergmann & Ganso (1965), Bergmann & Wiesner (1982), Bringeland (1981), Ceriani (1991), Cramp (1985), Creutz & Zschoke (1992), Crocq (1984), Duquet (1997), Étchécopar & Hüe (1978), Ficker (1990), Flint *et al.* (1984), Forsman (1998), Friedrich (1997), Galeotti *et al.* (1993), Gleixner *et al.* (1992), Gödecke & Rudat (1984), Golodushko & Samusenko (1961), Hagemeijer & Blair (1997), Handrinos & Akriotis (1997), Hormann & Menning (1997), Jakobsen (1978), Jedrzejewska & Jedrzejewski (1993), Kalberer & Kalberer (1980), Källander (1975), Kellomäki (1977), Klaus, Klaus & Bräsecke (1982), Klaus, Kucera & Wiesner (1976), Klaus, Vogel & Wiesner (1965), Kloubec (1992), König (1968, 1977, 1993, 1998), König *et al.* (1995), Korpimäki (1992a), Kullberg (1995), Laferrière (1952), Mattes (1981), Menning (1990, 1998), Mikkola (1983), Missbach (1976), Möckel & Möckel (1980, 1984), Möckel *et al.* (1992), Nadler (1994, 1996), Pacenovsky (1990, 1993), Pfennig (1995), Pühringer (1990, 1992), Rogacheva (1992), Rudat & Gödecke (1997), Rutgers & Norris (1972), Säman (1975), Scherzinger (1970, 1974a), Schöner (1976a, 1976b, 1980), Schulenberg (1992), Schulenberg & Wiesner (1986), Simeonov *et al.* (1990), Snow & Perrins (1998), Solheim (1984a, 1984b), Sonneborn & Daus (1995), Stepanyan (1990), Tonko (1992), Varga (1992), Voous (1988), Wendt (1997), Wiesner (1997a, 1997b), Wiesner & Rudat (1983), Wiesner *et al.* (1992), Ytreberg (1997), Zhao Zhengjie (1995), Zschoke (1982).

120. Collared Owlet

Glaucidium brodiei

French: Chevêchette à collier **German:** Wachtelkauz **Spanish:** Mochuelo Acollarado
Other common names: Pygmy Owl/Owlet, Collared Pygmy Owllet, Collared/Banded Pygmy-owl

Taxonomy. *Noctua Brodiei* Burton, 1836, Simla, Himalayas.

Sometimes considered to form superspecies with *G. passerinum*, *G. perlatum*, *G. californicum* and *G. gnoma* (including recently separated *G. cobanense* and *G. hoskinsii*), but DNA evidence clearly shows that *G. passerinum* and *G. californicum* are not closely related. Four subspecies recognized.

Subspecies and Distribution.

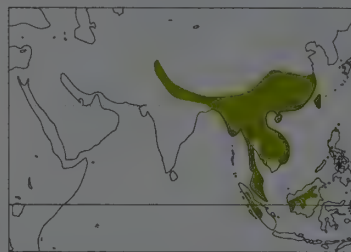
G. b. brodiei (Burton, 1836) - from N Pakistan through Himalayas to SE Tibet, N Indochina, S, C & E China (including Hainan), and S to Malaysia.

G. b. pardalotum (Swinhoe, 1863) - Taiwan.

G. b. peritum (Bonaparte, 1850) - Sumatra.

G. b. borneense Sharpe, 1893 - Borneo.

Descriptive notes. 15-17 cm; male c. 53 g, female c. 63 g. Tiny owl with rounded head, large for size of body. Rufous, chestnut and grey-brown morphs occur. Crown spotted creamy-buff, with staring "dorsal face" on nape; white eyebrows, white throat patch; back, tail and flight-feathers barred dark brown and buff; scapulars tipped white, forming interrupted lines down sides of mantle; breast sides and flanks barred, belly sides streaked; iris golden-yellow; bill greenish-horn; tarsi feathered white; feet greenish-yellow. Resembles a miniature version of the partially



Food and Feeding. Small birds, insects, rodents, lizards and skinks. Relative to size of owl, fairly large birds taken, including adult and nestling barbets (*Capitonidae*), woodpeckers (*Picidae*) and thrushes (*Turdidae*); often takes nestlings. One of most diurnal members of genus; active around dusk and at night, but also hunts all hours of day. Hunts from perch, such as fence post; swoops to catch insects in flight. Holds larger prey with foot while tearing at it with bill. Often mobbed by passerines.

Breeding. May-Jun in Nepal; Apr-May elsewhere in range. Nest unlined tree cavity; often kills woodpeckers or barbets to appropriate nest cavity. Usually 4 eggs (3-6); incubation c. 25 days; eggs hatch asynchronously; both adults feed nestlings.

Movements. Resident; some altitudinal movements suspected.

Status and Conservation. Not globally threatened. CITES II. Common to fairly common over most of range. Occurs in several protected areas throughout its range, such as Khao Yai and Kaeng Krachan National Parks (Thailand), Hsitung Forest Recreation Area (Taiwan), Kerinci-Seblat National Park (Sumatra) and Mount Kinabalu National Park (Borneo); frequently recorded at Fraser's Hill, Peninsular Malaysia. Mainly a forest bird, only occasionally observed near human habitation, so presumably vulnerable to effects of habitat destruction.

Bibliography. Ali & Ripley (1981), Ali *et al.* (1996), Bangs & Van Tyne (1931), Bates & Lowther (1952), Deignan (1945), Étchécopar & Hüe (1978), Glenister (1951), Grimmett *et al.* (1998), Holmes (1996), Hüe & Étchécopar (1970), Inskipp & Inskipp (1991), Lekagul & Round (1991), MacKinnon & Phillips (1993), Madoc (1976), Majumdar *et al.* (1992), van Marle & Voous (1988), Medway & Wells (1976), Riley (1938), Ripley (1982), Roberts (1991), Smythies (1981, 1986), Stepanyan (1995), Voous (1988), Wells (1999), Zhang Cizu *et al.* (1997), Zhao Zhengjie (1995).

121. Pearl-spotted Owl

Glaucidium perlatum

French: Chevêchette perlée **German:** Perlkauz **Spanish:** Mochuelo Perlado
Other common names: Pearl-spotted Owl

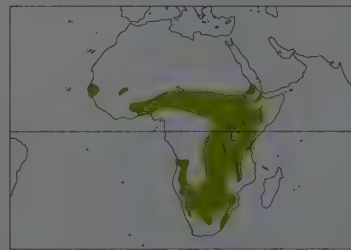
Taxonomy. *Strix perlata* Vieillot, 1817, Senegal.

Sometimes considered to form superspecies with *G. passerinum*, *G. brodiei*, *G. californicum* and *G. gnoma* (including recently separated *G. cobanense* and *G. hoskinsii*), but DNA evidence clearly shows that *G. passerinum* and *G. californicum* are not closely related. Population of E & NE Africa sometimes separated as *kilimense*, included in *licua*. Two subspecies recognized.

Subspecies and Distribution.

G. p. perlatum (Vieillot, 1817) - Senegambia to W Sudan; possibly also Liberia.

G. p. licua (Lichtenstein, 1842) - E Sudan, Ethiopia and Uganda S to N & E South Africa, Angola and Namibia.



Descriptive notes. 17-20 cm; wingspan c. 40 cm; male 36-86 g, female 61-147 g. Head cinnamon-brown with off-white facial disc, whitish eyebrows; nape has 2 black patches rimmed and interconnected with white, forming "false eyes"; upperparts also cinnamon-brown, with white spots; flight-feathers dark brown with light rufous bars; relatively long, brown tail showing incomplete white bars; breast and belly white with broad brown streaks, streaking denser on breast; yellow eyes and pale yellow-horn bill. Juvenile less rufous, with fewer spots on mantle and crown, shorter tail. Race *licua* greyer and more heavily spotted than

nominate. **VOICE.** Series of loud whistles rising in pitch and volume to climax of long, loud notes; female higher-pitched than male; vocal mainly after dark, often duetting.

Habitat. Commonest in bushveld and open woodland, but also occurs in grassland, forest and dense woodland.

Food and Feeding. Mainly arthropods; also bats, birds, rodents and lizards. Most diurnal African owl, especially in winter, but hunts mainly at night. Hunts from perch, watching ground for prey; flicks tail when excited or nervous; dives fast to strike; strong, powerful feet capable of killing birds larger than itself, such as doves (*Columbidae*). "False face" most prominent when head cocked forwards to look for prey beneath perch; may serve to discourage predators attacking from behind, or make small birds believe it is looking away, rendering them more vulnerable to surprise attacks. Also chases prey in flight, which is fast and undulating as in woodpeckers (*Picidae*). Once observed pirating food from wood-hoopoes (*Phoeniculus*) as they carried it to nest; suspected of robbing nest holes and eating carrion.

Breeding. Lays Aug-Nov, peak Sept-Oct. Territorial throughout year. Nest in cavity, especially old nest of barbet (*Capitonidae*) or woodpecker, 1.2-10 m above ground; will reuse nest-site; sometimes ravages nests of other species to gain site, but at other times itself usurped by bees or by other birds such as hornbills (*Bucerotidae*), rollers (*Coraciidae*) or starlings (*Sturnidae*). Female sometimes calls to solicit courtship feeding a month before laying, often followed by copulation; also sexes call in duet. 3 eggs (2-4), incubated by female while male feeds; incubation c. 29 days, eggs hatch asynchronously; fledging period c. 31 days; if disturbed at nest, female sits tight and lies flat on nest floor, looking like nest debris and showing "false face". Rarely raises full clutch to fledging; in 8 pairs, none had 100% success; no second broods recorded.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Widespread; locally common to rare in various parts of range. Most commonly observed owl in S Africa, probably as a result of diurnal habits. Less common in upper W edge of range; only report from Liberia was of adult with half-

grown nestling brought to Monrovia Zoo; in Ghana uncommon, confined to woodland savanna. Few records from L. Victoria Basin.

Bibliography. Ash & Miskell (1998), Bannerman (1953), Barlow *et al.* (1997), Baron & Baron (1976), Benson & Benson (1977), Benson *et al.* (1971), Cave & Macdonald (1955), Cheke & Walsh (1996), Clancey (1980a), Dixon (1981), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Elgood *et al.* (1994), Farmer (1984), Friedmann (1930), Fry *et al.* (1988), Gatter (1997), Ginn *et al.* (1989), Giraudoux *et al.* (1988), Gore (1990), Grimes (1987), Harrison *et al.* (1997), Irvine & Irvine (1991), Kemp & Calburn (1987), Kemp & Kemp (1998), Lewis & Pomeroy (1989), Lorber (1984), Mackworth-Præd & Grant (1957, 1962, 1970), Maclean (1993), Madden (1983), Mendelsohn (1989), Penry (1994), Pickford *et al.* (1989), Pinto (1983), Scherzinger (1977), Short *et al.* (1990), Snow (1978), Steyn (1979, 1982, 1984, 1994b), Zimmerman, D.A. *et al.* (1996).

122. Northern Pygmy-owl

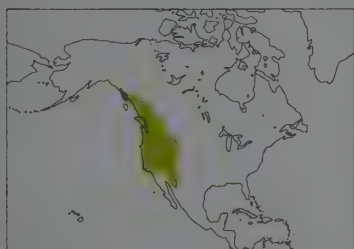
Glaucidium californicum

French: Chevêchette des Rocheuses **German:** Kalifornienzwergkauz **Spanish:** Mochuelo Californiano
Other common names: Californian Pygmy-owl

Taxonomy. *Glaucidium californicum* P. L. Selater, 1857, Calaveras County, California. Sometimes considered to form superspecies with *G. passerinum*, *G. brodiei*, *G. perlatum* and *G. gnoma* (including recently separated *G. cohanense* and *G. hoskinsii*), but DNA evidence clearly shows that present species and *G. passerinum* are not closely related. Formerly treated as race of *G. gnoma*; split on basis mainly of vocalizations, DNA and ecology. Racial differences rather slight, based primarily on morphology; *pinicola* perhaps not valid. Four subspecies recognized.

Subspecies and Distribution.

G. c. grinnelli Ridgway, 1914 - SE Alaska through coastal British Columbia S to coastal W USA (Washington, Oregon, California).
G. c. swarthi Grinnell, 1913 - Vancouver I.
G. c. californicum P. L. Selater, 1857 - British Columbia and Alberta to W USA (S to Nevada and California) and NW Mexico (N Sonora, NW Chihuahua).
G. c. pinicola Nelson, 1910 - W USA (Idaho and Montana S to Arizona and New Mexico, E to Colorado).



Descriptive notes. 16-18 cm; male 62 g, female 73 g (*californicum*). Plump, with round head, short wings and long tail; fairly tame, easily approached; flight undulating, with distinct flapping and gliding. Grey and rufous morphs occur. Facial disc brownish-white, not well defined; upperparts grey-brown with fine whitish spots on head, nape, mantle, scapulars and wing-coverts; back of head shows pattern resembling eyes or face, showing "false eyes" of black centres and white borders and slight suggestion of bill; tail barred thinly white, separated by wider brownish bars; whitish underparts with brownish-black streaks, sides of

chest and flanks brownish, with fine white spotting; eyes yellow, bill whitish-yellow; tarsus fully feathered. Differs from *G. brasilianum* in distinct spotting on head; from *G. minutissimum* in streaking on back; from *Aegolius funereus* and *A. acadicus* in smaller head, indistinct facial disc, and longer tail extending past wings when perched. Sexual dichromatism reported, males averaging greyer than females; needs further study. Juvenile has incomplete spotting on head over eyebrows, little to no spotting on back, dark bill. Races differ slightly in tone of coloration and degree of spotting; *swarthi* very dark; *pinicola* perhaps more spotted. **VOICE.** Usually series of single and evenly spaced "toot" notes, often following staccato sequence; in Colorado, heard to produce extended series of hoots, about 2 per second for periods of up to 20 seconds.

Habitat. Coniferous and deciduous forest and forest edge; in Sierra Nevada of California, extends from blue oak (*Quercus*) savanna habitats in foothills to mixed montane conifer forest, becoming scarce above 1800 m and preferring sites with low to intermediate canopy coverage, such as edges of meadows, lakes and similar clearings. In Arizona, *pinicola* associated primarily with montane coniferous forest. In California, breeding males collected from forest of mature, residual and second-growth pine, especially ponderosa pine (*Pinus ponderosa*), incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*) and black oak (*Quercus velutina*), ranging from 1200 m to 2190 m in elevation.

Food and Feeding. Small to medium-sized birds, mammals and large insects; to lesser extent, amphibians and reptiles. Mammals include mice (*Microtus*, *Peromyscus*) and shrews (*Sorex*), and birds include grosbeaks (*Coccothraustes*) and swallows (*Tachycineta*); also California Quail (*Callipepla californica*) and red squirrel (*Tamiasciurus*) prey items of interest because of size in relation to that of species; insects include beetles and moths. One study found that sexes ate similar percentages of vertebrate prey (males 85%, females 76%); however, females ate significantly more small mammals than males, which fed more on birds. In Montana, prey deliveries to nest reported to comprise 65% mammals, 32% birds and 3% insects; in only comprehensive study of diet, fed on 36% birds; also, 2 individuals were caught in mist-nets with partially eaten Dusky Flycatcher (*Empidonax oberholseri*), Black-capped Chickadee (*Parus atricapillus*), MacGillivray's Warbler (*Opornis tolmiei*) and Common Yellowthroat (*Geothlypis trichas*). Diurnal and probably crepuscular; activity probably dictated by hunger, prey densities and nesting stage. When hunting, uses perch-and-pounce technique; appears to hunt by sight, but prey location by sound cannot be ruled out; when foraging, will focus on prey and switch tail from side to side in quick, jerky motion (significance unknown), then move closer to prey in zigzag pattern from branch to branch, until dropping straight down on prey. Captives concentrated on breast of birds and ate entire body of small mammals; most prey decapitated; usually half of prey eaten, then other half about 3-6 hours later; will cache and later retrieve food; observed picking and pulling road-killed Pine Siskins (*Carduelis pinus*) off highway and caching in nearby tree; caching may buffer and reduce food shortages during inclement weather, or increase foraging opportunities during activity periods.

Breeding. Season Apr-Aug. Apparent seasonal monogamy; no reports of polygyny. Nest in cavity, usually unlined, though nest cavity in Canada was lined with strip of western red cedar (*Thuja plicata*); recorded nesting with *Aegolius acadicus* in same snag, also with Pileated Woodpecker (*Dryocopus pileatus*); reuse of nest not well known. In courtship, female may solicit male with tooting call, hitherto generally thought to be male behaviour; further study needed. 2-7 eggs; incubation c. 28 days; hatching asynchronous, though some reports suggest more synchronous than in open-nesting strigids; chicks semi-altricial, dependent on female for food and thermoregulation; male feeds incubating and brooding female until nestlings c. 9 days old, when female begins hunting; fledging c. 23 days, all leaving about same time, lending support to suggestion of more synchronous hatching, though further study needed; fledglings observed to roost on same branch 75 m

from nest 8 days after leaving. Age of first breeding probably 1 year. Lifespan and survivorship unknown (no ringing recoveries, despite 318 birds ringed up to 1994).

Movements. Partly resident, also either migratory or wandering. Long-distance movements unknown; local movements apparent in W USA (Rocky Mts); e.g., in W Montana valleys, birds show up Nov and leave Mar; appears to be vertical migrant, but studies needed to confirm this.

Status and Conservation. Not globally threatened. CITES II. Non-significant decline in California; non-significant increase in Oregon; significant decline in interior Rocky Mts (Wyoming, Montana, Idaho, British Columbia and SE Alberta); on larger geographic scale, no significant increase for W USA or North American continent. In Canada, current population size ranges from 2000 to 10,000 pairs. Although much apparently suitable habitat throughout range, much of this unoccupied by species, perhaps indicating that factors beyond prey species important to distribution and abundance. Probably affected by predators, other forms of natural mortality, prey densities and catastrophic events such as weather, among other variables; also, possibility of secondary poisoning via pesticides (organochlorines) must be considered. As forest species and obligate cavity nester, probably vulnerable to some forestry practices and development; habitat alterations affecting cavity-excavators and prey species would be likely to affect species. Not known to use nestboxes. Management suggestions include long-term monitoring, research, defining and maintaining forest habitats, and public education.

Bibliography. Armstrong (1983), Babeock (1993), Bourcious (1987), Bull, Hohmann & Henjum (1987), Campbell *et al.* (1990), Eckert (1974), Gent (1984), Hayward (1983), Hayward & Garton (1988), Heidrich *et al.* (1995a), Heintzelman (1992), Hewkin (1993), Holt & Hillis (1987), Holt & Leroux (1996), Holt & Norton (1986), Holt *et al.* (1990), Howell & Webb (1995a), Johnson (1988), Kaufman (1996), Lundsten (1993), Marti (1986), Munn (1997), Norton & Holt (1982), Price *et al.* (1995), Righter (1995), Root (1988), Small (1994), Stotz *et al.* (1996), Tyler & Phillips (1978), Urban (1959), Voous (1988), Walker (1993), Walsh (1990), Webb (1982a), Wolfe & de la Torre (1990).

123. Mountain Pygmy-owl

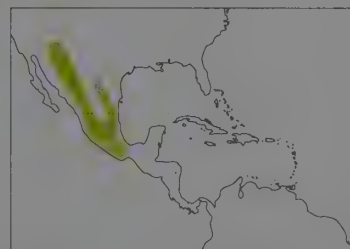
Glaucidium gnoma

French: Chevêchette naine **German:** Gnomenkauz **Spanish:** Mochuelo Gnomo
Other common names: Northern Pygmy-owl(!), American/Mexican Pygmy-owl

Taxonomy. *Glaucidium Gnoma* Wagler, 1832, Mexico.

Sometimes considered to form superspecies with *G. passerinum*, *G. brodiei*, *G. perlatum* and *G. californicum*, and including recently separated *G. cohanense* and *G. hoskinsii*, but DNA evidence clearly shows that *G. passerinum* and *G. californicum* are not closely related. Formerly considered to include last 3 as races, but these split on basis of vocalizations and/or DNA evidence. Perhaps closely related to *G. costaricanum*, which has recently been considered conspecific with present species by some authors. Monotypic.

Distribution. From SE Arizona S through interior highlands of Mexico (from Chihuahua and Coahuila S to Oaxaca).



Descriptive notes. 15-17 cm; 54-73 g. Very similar to *G. californicum*. Differs in slightly smaller size, shorter tail, and voice. **VOICE.** Song of "toots" usually given in groups of 2 in series, interspersed with single notes; often starts with rapid sequence of short "hu" notes.

Habitat. Coniferous forest and forest edge in mountain regions, generally above 1500 m; in Arizona, however, typically on S-facing mountain slopes dominated by oaks (*Quercus*).

Food and Feeding. Similar to that of *G. californicum*. Mainly insects, especially beetles, grasshoppers and crickets; also small mammals, birds and reptiles.

Breeding. Season Apr-Aug. Apparent seasonal monogamy; no reports of polygyny. Nest in tree cavity, especially old hole of woodpecker. 2-4 eggs; incubation c. 28 days; hatching asynchronous; male feeds incubating and brooding female until nestlings about 9 days old, when female begins hunting; fledging probably c. 23 days. Age of first breeding probably 1 year; life span and survivorship unknown; no ringing recoveries.

Movements. Presumed resident.

Status and Conservation. Not globally threatened. CITES II. Apparently not uncommon locally. Has been recently recorded at Cerro El Potosi (Nuevo León), Barranca Rancho Liebre (Sinaloa), Volcán de Fuego (Jalisco), Temascaltepec (México), Sierra de Atoyac (Guerrero), and Cerro San Felipe (Oaxaca). Factors affecting populations, and suggestions for management, similar to those for *G. californicum*.

Bibliography. Baichich & Harrison (1997), Binford (1989), Eckert (1974), Heidrich *et al.* (1995a), Heintzelman (1992), Howell & Webb (1995a), Johnson (1988), Kaufman (1996), Root (1988), Schaldach (1963), Stotz *et al.* (1996), Tyler & Phillips (1978), Voous (1988), Walker (1993), Wolfe & de la Torre (1990).

124. Guatemalan Pygmy-owl

Glaucidium cohanense

French: Chevêchette du Guatemala **Spanish:** Mochuelo Guatemalteco
German: Guatemalazwergkauz

Taxonomy. *Glaucidium cohanense* Sharpe, 1875, Cobán, Alta Vera Paz, Guatemala.

Sometimes considered to form superspecies with *G. passerinum*, *G. brodiei*, *G. perlatum*, *G. californicum*, *G. gnoma* and *G. hoskinsii*, but recent DNA evidence clearly shows that *G. passerinum* and *G. californicum* are not closely related. Has usually been considered a race of *G. gnoma*, but separation from latter perhaps currently unwarranted, as vocalizations undescribed. Monotypic.

Distribution. S Mexico (Chiapas), Guatemala and Honduras.

Descriptive notes. 16-18 cm. Bright reddish-brown, with little mottling on head; wings spotted and barred; tail long with 5-8 white bars; rufous streaks below broad, rather diffuse; iris and feet yellow. Occurs also in brown



morph. Juvenile similar to adult, but head grey with forehead more mottled. Voice. No information available.

Habitat. Highland forest.

Food and Feeding. Insects, small rodents and occasionally birds.

Breeding. Little known. Nest in abandoned woodpecker hole; 3-4 eggs.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in North Central American highlands EBA. Little known about ecology and population status. Recently recorded in Mexico, near the towns of Unión Juárez and San Cristóbal de las Casas, Chiapas. Forest destruction possibly a threat.

Bibliography. Anon. (1998a), Heidrich *et al.* (1995a), Howell (1995), Howell & Webb (1995a), Land (1970), Monroe (1968), Ridgely & Gwynne (1989), Stotz *et al.* (1996), Voous (1988), Walters (1993).

125. Baja Pygmy-owl

Glaucidium hoskinsii

French: Chevêchette de Hoskins

Spanish: Mochuelo de Hoskins

German: Hoskinszwegkauz

Other common names: Cape Pygmy-owl

Taxonomy. *Glaucidium gnoma hoskinsii* Brewster, 1888, Sierra de la Laguna, Miraflores, Baja California.

Sometimes considered to form superspecies with *G. passerinum*, *G. brodiei*, *G. perlatum*, *G. californicum*, *G. gnoma* and *G. cobanense*, but DNA evidence clearly shows that *G. passerinum*

and *G. californicum* are not closely related. Formerly treated as race of *G. gnoma*; recently split on basis mainly of vocalizations. Monotypic.

Distribution. S Baja California (Mexico): Sierra Victoria, probably also Sierra de la Giganta.



Descriptive notes. 15-16 cm; c. 50-65 g. Tiny, like *G. gnoma*; apparently monomorphic. Sandy grey-brown overall, averaging redder in female; facial disc brownish, white eye-brows narrow; crown, nape and upperparts grey-brown to rufous-brown, spotted buffy. Juvenile undescribed; probably differs from adult in same way as do *G. californicum* and *G. gnoma*. Voice. Slow double hoots with occasional single hoots; also rapid, slightly quavering "huhuhu", which often precedes bouts of hooting.

Habitat. Pine and pine-oak forest, from 1500-2100 m; descends to 500 m in winter, prob-

ably also to deciduous woodland.

Food and Feeding. Insects and reptiles, as well as small mammals and birds.

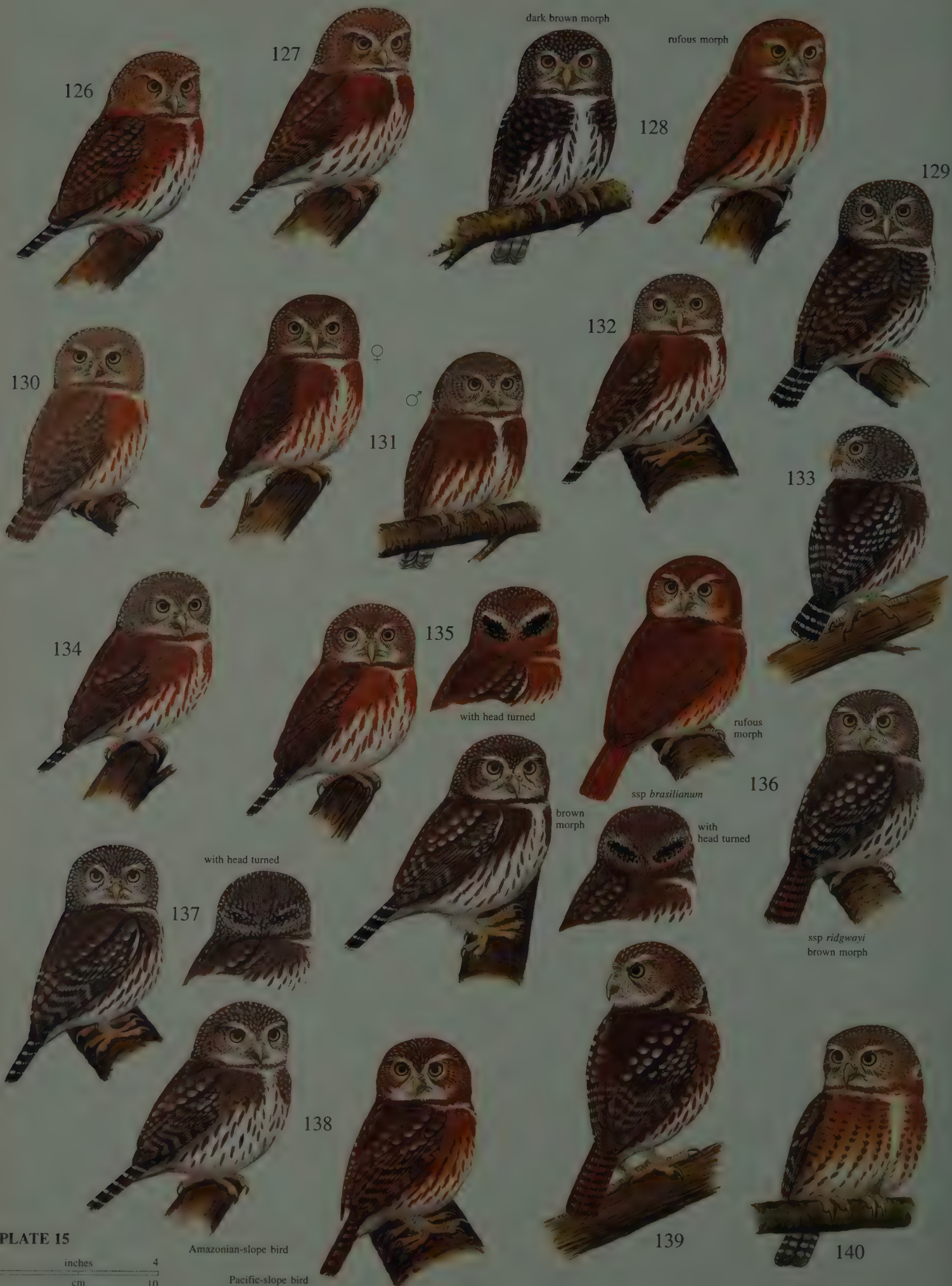
Breeding. Little known. Lays May-early Jun; juvenile observed in late Jul. Nest in tree cavity.

Movements. Rare winter visitor Oct-Mar to N Baja California.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Baja California EBA. Considered fairly common. Has been recently recorded in Sierra de la Laguna and at the edge of the small town of Miraflores. Little known about ecology and population status.

Bibliography. Anon. (1998a), Heidrich *et al.* (1995a), Howell & Webb (1995a), Stotz *et al.* (1996), Wilbur (1987).

PLATE 15



126. Costa Rican Pygmy-owl

Glaucidium costaricanum

French: Chevêchette du Costa Rica

Spanish: Mochuelo Costarricense

German: Costa-Rica-Zwergkauz

Taxonomy. *Glaucidium jardinii costaricanum* L. Kelso, 1937, Costa Rica.

Formerly treated as race of *G. jardinii*, but clearly different from latter in vocal patterns. Has recently been considered by some authors as conspecific with *G. gnoma*; probably related to the recently discovered *G. nubicola*; further study required. Monotypic.

Distribution. C Costa Rica to W Panama, possibly to E Panama.



Descriptive notes. c. 15 cm. Strongly patterned tiny owl. Head brown, crown densely dotted white, face barred buff, eyebrows and lores white; back of head shows pattern of black "false eyes"; nuchal collar rufous; upperparts dark brown, scapulars and wing-coverts boldly spotted buffy-white; flight-feathers and tail barred; underparts white, streaked black, sides of breast rich brown with buff barring and whitish spots. Similar to *G. gnoma*; differs in somewhat smaller size, darker upperparts contrasting with heavily spotted paler crown, and darker tail. Occurs in brown and rufous morphs; latter with sparser buffy spotting, and some birds

nearly unspotted. **Voice.** Long series of whistled double "poop-poop" notes, sometimes 3 pairs of notes only; when excited, 5 higher-pitched "poop" notes in very rapid succession.

Habitat. Upland forest, mainly of pine-oak; prefers canopy and edge of forest; also in semi-open areas adjacent to forest, including pastures with scattered trees. Middle to high elevations, from timber-line down to c. 900 m on Caribbean slope, and to 1200 m on Pacific slope.

Food and Feeding. Mainly insects and small vertebrates, including birds and lizards. Perch-and-pounce predator, flying swiftly to perch in dense foliage, watching actively, and attacking in short, swift dash; if attempt fails, will usually return to perch rather than pursue.

Breeding. Lays Mar in Costa Rica; in cavity in tree, perhaps most often old woodpecker hole; 1 nest 2 m above ground in dead stub of pasture tree; 3 eggs recorded.

Movements. Presumably resident.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Costa Rica and Panama highlands EBA. Considered rare to locally (e.g. Cerro de la Muerte) fairly common in Costa Rica; rare in Panama.

Bibliography. Anon. (1998a), Heidrich *et al.* (1995a), Kelso (1937), Marín & Schmitt (1991), Ridgely & Gwynne (1989), Slud (1964), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968a).

127. Cloudforest Pygmy-owl

Glaucidium nubicola

French: Chevêchette des nuages

German: Nebelzwergkauz

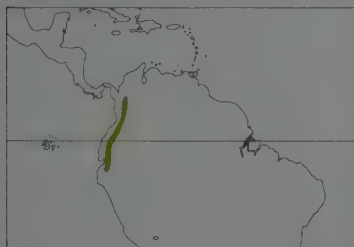
Spanish: Mochuelo Ecuatoriano

Other common names: Ecuadorian Pygmy-owl

Taxonomy. *Glaucidium nubicola* Robbins and Stiles, 1999, south side of Quebrada San José de the Río Blanco, Carchi Province, Ecuador.

Recently discovered species; probably long overlooked as a result of morphological similarity and geographical proximity to *G. jardinii*, but vocally very distinct and also exhibits subtle but constant morphological differences. Probably most closely related to *G. gnoma* and *G. costaricanum*. Monotypic.

Distribution. W slope of Andes in Colombia (Cordillera Central) and Ecuador.



Descriptive notes. c. 16 cm; c. 76-80 g. Similar to *G. gnoma* and *G. costaricanum*. Differs in shorter tail, less extensive spotting on mantle and back, unspotted breast sides; has concealed white nuchal collar; most spots on scapulars and upperwing-coverts tinged with pale rufous. Irides yellow, bill greenish-yellow, tarsi and toes yellow, claws black. **Voice.** Series of paired whistled notes, each separated by c. 0.2 seconds, with intervals between pairs 0.32-0.37 seconds.

Habitat. Wet primary cloudforest, on steep slopes, at elevations of 1400-2000 m.

Food and Feeding. Stomach contents included insects (orthopterans and hemipterans) and a small lizard; probably also takes small birds.

Breeding. Season probably Feb-Jun. No other information.

Movements. Presumably resident.

Status and Conservation. Not globally threatened. CITES II. Species little known, and no data on population level. Continuing forest destruction and degradation a major threat; most of W Ecuador, including species' type locality, completely deforested; major road construction in W Colombia is providing access to once remote areas and resulting in similar degree of deforestation. Several protected areas occur within geographical and altitudinal range of species, i.e. Los Farallones and Munchique National Parks, La Planada Nature Reserve and Río Nambi Community, in Colombia, and Cotacachi-Cayapas, Los Cedros and Maquipucuna Reserves, in Ecuador.

Bibliography. Robbins & Stiles (1999).

128. Andean Pygmy-owl

Glaucidium jardinii

French: Chevêchette des Andes

German: Andenzwergkauz

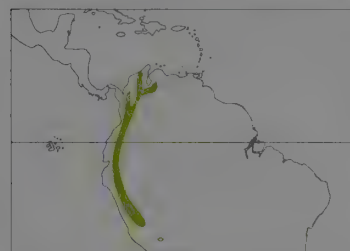
Spanish: Mochuelo Andino

Other common names: Jardine's Pygmy-owl

Taxonomy. *Palaeopsis jardinii* Bonaparte, 1855, Andes of Quito, Ecuador.

Suggested as forming superspecies with *G. bolivianum*. Has been treated as conspecific with *G. brasilianum*, or by some authors as race of *G. gnoma*; differs from both in voice, coloration and ecology. Formerly considered to include *G. costaricanum* as race, but latter now shown to be very distinct. Monotypic.

Distribution. From N Colombia and W Venezuela S through Ecuador to C Peru.



Descriptive notes. 14.5-16 cm; 65 g. Tiny, with small head and ill-defined mask; normally looks round-headed. Dimorphic, either dull dark brown with white marks, or dark chestnut with buff marks; crown has numerous small white dots (normally not streaks); short eyebrows, moustaches and broad throat patch white; nape shows conspicuous black-and-white face-like pattern; back and wings with large but scattered white spots; tail black with c. 5-6 white or buff bars; underparts boldly marked, dark breast sides with some short pale spots or bars, flanks and belly with coarse dark streaks; eyes yellow. Differs from *G. nanum* in

darker face, and shorter tail with fewer bars; from *G. brasilianum* in barring or spotting on chest sides. Juvenile with crown and nape unmarked, or has thin streaking in these areas. **Voice.** In Colombia, long series of whistled double "poop-poop" calls; in Peru, long series of evenly spaced single "poop" calls, often prefaced by c. 2 introductory whistles.

Habitat. Semi-arid to humid open cloudforest and elfin forest; montane or highland forest and adjacent semi-open land; wooded ravines with transition to swampy or grassy habitats; occupies forest canopy and middle levels, as well as forest edge; sometimes pastures with scattered trees. Occurs at 900-4000 m; in Colombia 2100-2800 m.

Food and Feeding. Birds and large insects; takes more birds than other pygmy-owls, sometimes of nearly its own size. Nocturnal and diurnal; frequently mobbed by other birds.

Breeding. In Colombia, male found in breeding condition in late Dec; nest and eggs observed in Mar. Nest in tree cavity, perhaps most often woodpecker hole.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Widespread; considered fairly common. Occurs in several protected areas throughout its range, such as Las Cajas National Recreation Area and Podocarpus National Park, both in Ecuador. Needs at least patchy forest, but little information available; probably vulnerable to forest destruction.

Bibliography. Baez *et al.* (1997), Coats (1979), Ejdlsá & Krabbe (1990), Heidrich *et al.* (1995a), Hilty & Brown (1986), König (1991b), Meyer de Schauensee & Phelps (1978), Miller (1963), Olrog (1968), Stotz *et al.* (1996).

129. Yungas Pygmy-owl

Glaucidium bolivianum

French: Chevêchette des yungas

German: Bolivienzwergkauz

Spanish: Mochuelo Boliviano

Taxonomy. *Glaucidium bolivianum* König, 1991, Salta, Argentina.

Suggested as forming superspecies with *G. jardinii*. Monotypic.

Distribution. E slope of Andes in SE Peru, WC Bolivia and NW Argentina.



Descriptive notes. c. 16 cm; male c. 55 g. Similar to *G. jardinii*. Differs in more densely spotted crown, usually more barred chest sides and shorter flank streaks. Occurs in brown, grey and rufous morphs. Juvenile with unmarked crown, flank streaks more diffuse. **Voice.** 2 or 3 whistled notes followed by trill, then rather slow series of equally spaced hollow notes; often omits first part, utters just the slow series for long periods.

Habitat. Montane forest and cloudforest; partial to *Alnus* groves with dense undergrowth and areas with heavy presence of thick moss and epiphytes; also *Podocarpus* forest. Usually high in the canopy or at middle levels. From 1400 m to 3000 m, locally down to 900 m.

Food and Feeding. Insects, small birds, possibly also reptiles. Nocturnal and diurnal, perhaps more so during cloudy wether.

Breeding. Nest in old woodpecker hole; no other information.

Movements. No information. Probably resident, though might perform some altitudinal movements.

Status and Conservation. Not globally threatened. CITES II. Appears to have declined in few years since first described. Forest destruction and degradation probably main threat, though inaccessibility of parts of range should afford some protection. Occurs in several protected areas through range, e.g. Cotapata National Park, La Paz (Bolivia), and Callegua National Park, Jujuy (Argentina); in latter, considered fairly common.

Bibliography. Canevari *et al.* (1991), Chebez (1994), Ejdlsá & Mayer (1996), Heidrich *et al.* (1995a), König (1991b), Krabbe *et al.* (1996), Martínez (1998), Stotz *et al.* (1996), Straneck, Ridgely & Rodríguez (1987)

130. Colima Pygmy-owl

Glaucidium palmarum

French: Chevêchette du Colima

German: Palmenzwergkauz

Spanish: Mochuelo de Colima

Taxonomy. *Glaucidium palmarum* Nelson, 1901, Tepic, Nayarit.

Considered member of *G. minutissimum* complex, which also includes *G. sanchezi*, *G. griseiceps*, *G. parkeri* and *G. hardyi*; further study needed to determine true relationships. Recently separated from *G. minutissimum* on basis of vocalizations. Racial differentiation uncertain, perhaps only individual variation or polymorphism. Three subspecies tentatively recognized.

Subspecies and Distribution.

G. p. oberholseri R. T. Moore, 1937 - S Sonora to S Sinaloa (NW Mexico).

G. p. palmarum Nelson, 1901 - Nayarit to Oaxaca (C Mexico).

G. p. grisei R. T. Moore, 1947 - SW Morelos and NE Guerrero (C Mexico).



Descriptive notes. 13-15 cm; male c. 45 g, female c. 50 g. Tiny; facial disc brownish, flecked white, with short whitish eyebrows; crown and nape greyish tawny-brown with extensive whitish to pale buff spotting, and slightly greyer than tawny olive-brown back; bars on wings formed by pale cinnamon to buffy-white spots; tail with 6-7 white bars. Juvenile has unspotted grey crown and nape contrasting with brown upperparts; forehead sometimes flecked whitish to buff, tail-bars pale buffy-cinnamon. **VOICE.** Song comprises 2-24 short hoots separated by long pauses; often successively increasing number of notes,

"hoo-hoo, hoo-hoo-hoo, hoo-hoo-hoo-hoo..."

Habitat. Tropical semi-deciduous forest (tropical forest), usually in foothills; locally pine-oak forest and coffee plantations from sea-level to 1500 m.

Food and Feeding. Birds, reptiles and large insects.

Breeding. Lays during May. Nest in tree cavity, often woodpecker hole; 2-4 eggs.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Fairly common to common within range, but little quantitative information available; data regarding status, population size and ecology required. Localities where species has recently been recorded include San Blas and Cerro de San Juan (Nayarit), Barranca El Choncho (Jalisco), Cañón de Lobos (Morelos), and La Soledad and Puerto Escondido (Oaxaca).

Bibliography. Anon. (1998a), Binford (1989), Buchanan (1964), Heidrich *et al.* (1995a), Howell & Webb (1995a), Schaldach (1963), Stotz *et al.* (1996), Voous (1988).

131. Tamaulipas Pygmy-owl*Glaucidium sanchezi*

French: Chevêchette du Tamaulipas

Spanish: Mochuelo Tamaulipeco

German: Sanchezzwergkauz

Taxonomy. *Glaucidium sanchezi* Lowery and Newman, 1949, San Luis Potosí, Mexico.

Considered member of *G. minutissimum* complex, which also includes *G. palmarum*, *G. griseiceps*, *G. parkeri* and *G. hardyi*; further study needed to determine true relationships. Recently separated from *G. minutissimum* on basis of vocalizations. Monotypic.

Distribution. NE Mexico (S Tamaulipas, SE San Luis Potosí and extreme N Hidalgo).



Descriptive notes. 13-18 cm; male c. 53 g. Sexual dimorphism unique in genus. Male has grey-brown crown and nape, with fine pale buff to whitish spots on forehead; nape with dark "false eyes", ground colour contrasts slightly with greyish olive-brown back; bars on wings formed by pale cinnamon to pale buff spots; tail has 6 whitish bars. Female has crown, nape and upperparts washed cinnamon, dorsally fairly uniform and distinctly redder than male; tail-bars buff to pale cinnamon. Juvenile with unspotted grey crown and nape contrasting with brown upperparts; forehead can be flecked whitish to buff; "false eye-spots" sootier, tail-bars

pale cinnamon. **VOICE.** Song comprises 1-3 long, slow-paced, high-pitched hoots with long pauses between; differs from others of genus in fewer, longer notes with long inter-note intervals.

Habitat. Subtropical, humid evergreen and semi-deciduous forest, pine-evergreen forest, typically cloudforest. Occurs at 900-2100 m.

Food and Feeding. Large insects and reptiles.

Breeding. Little information. Nest in tree cavity or hole, especially old woodpecker hole; 2-4 eggs.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Southern Sierra Madre Oriental EBA. Uncommon to fairly common. Regularly recorded around the towns of Gómez Farías (Tamaulipas) and El Naranjo (San Luis Potosí). Little information available; data on status, population size and ecology required.

Bibliography. Anon. (1998a), Heidrich *et al.* (1995a), Howell & Robbins (1995), Howell & Webb (1995a), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Voous (1988).

132. Central American Pygmy-owl*Glaucidium griseiceps*

French: Chevêchette à tête grise

Spanish: Mochuelo Centroamericano

German: Graukopf-Zwergkauz

Taxonomy. *Glaucidium griseiceps* Sharpe, 1875, tropical lowlands of Alta Vera Paz, Guatemala. Considered member of *G. minutissimum* complex, which also includes *G. palmarum*, *G. sanchezi*, *G. parkeri* and *G. hardyi*; further study needed to determine true relationships. Recently separated from *G. minutissimum* on basis of vocalizations. Racial differentiation uncertain, more study required. Three subspecies tentatively recognized.

Subspecies and Distribution.

G. g. occultum R. T. Moore, 1947 - S Mexico (SE Veracruz, N Oaxaca and Chiapas).

G. g. griseiceps Sharpe, 1875 - Guatemala, Belize and Honduras.

G. g. rarum Griscom, 1931 - Costa Rica and Panama.

Descriptive notes. 13-18 cm; male c. 51 g, female c. 10% larger. Crown and nape brown-grey to grey-brown, forehead with fine pale buff to whitish spots (can extend back to nape), nape with dark "false eyes"; tail brown, with 2-4 broken whitish to pale buff bars on upperside and 2 pale bars visible on undertail; underparts whitish with rufous-brown streaking. Juvenile with unspotted grey crown and nape contrasting with brown upperparts; "false eye-spots" sootier, tail-bars pale cinna-



mon. **VOICE.** Song begins with 2-4 equally spaced hoots, followed by very brief pause, then series of 6-18 very similar notes, "hoo-hoo, hoo-hoo-hoo..."; trills may precede hooting series.

Habitat. Humid forest and adjacent tall secondary growth, semi-open areas, old cacao plantations. In lowlands and foothills: from sea-level to 800 m in Costa Rica, to 1200 m in Mexico and to 1300 m in Guatemala.

Food and Feeding. Large insects, reptiles such as lizards, small birds such as tanagers and honeycreepers (Thraupidae), and small mammals. Often hunts by day.

Breeding. Lays Apr-May. Nest in tree cavity or old woodpecker hole; 2-4 eggs.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. In Mexico generally uncommon but locally fairly common, e.g. near Valle Nacional (Oaxaca), and around the Mayan ruins of Palenque and Bonampak (Chiapas). Fairly common in Caribbean lowlands of Costa Rica, e.g. at Finca La Selva; scarcer and locally uncommon in Panama. Generally little known; data regarding status, population size and ecology desired.

Bibliography. Anon. (1998a), Binford (1989), Heidrich *et al.* (1995a), Hilty & Brown (1986), Howell & Webb (1995a), Janzen & Pond (1976), Land (1970), Monroe (1968), Olrog (1968), Ridgely & Gwynne (1989), Stotz (1960, 1964), Stiles & Skutch (1989), Stotz *et al.* (1996), Voous (1988), Wetmore (1968a).

133. Subtropical Pygmy-owl*Glaucidium parkeri*

French: Chevêchette de Parker

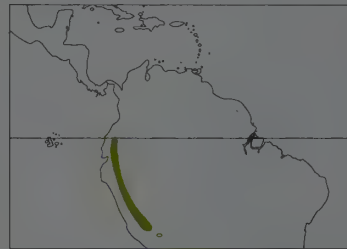
German: Parkerzwergkauz

Spanish: Mochuelo de Parker

Taxonomy. *Glaucidium parkeri* Robbins and Howell, 1995, Cerros del Sira (1550 m), Departamento Huánuco, Peru.

Considered member of *G. minutissimum* complex, which also includes *G. palmarum*, *G. sanchezi*, *G. griseiceps* and *G. hardyi*; further study needed to determine true relationships. Recently described species with highly distinctive song, possibly not closely related to others of that complex. Monotypic.

Distribution. E slope of Andes in Ecuador and Peru; possibly N to SW Colombia, possibly also extending farther S into N Bolivia.



Descriptive notes. 14 cm; c. 62 g. Tiny; crown and sides of face grey-brown, conspicuously spotted white; nape with prominent "false eyes" and concealed white nuchal collar; upperparts from mantle to rump dark brown; scapulars and upperwing-coverts dark brown, boldly spotted white, with dull olive-rufous wash to outer edges of wing-coverts and secondaries; primaries and secondaries dark brown with conspicuous, irregularly shaped white spots; tail blackish with 5 incomplete white bands; underparts from chin to undertail-coverts white, throat feathers tipped dark brown, and sides of chest medium brown;

broad, ill-defined, dull brownish olive-rufous streaks on lower chest, flanks and belly; bill greenish-yellow; eyes and toes yellow. Differs from other species of *G. minutissimum* complex in relatively large and distinct white spotting on crown, scapulars and upperwing-coverts, white (not buffish) wing-spots, less rufous ventral streaking. Juvenile undescribed. **VOICE.** Song consists of 2-4 relatively short, low-pitched hoots, with increasing length of inter-note pauses, especially between final 2 notes, "hu-hu, hu...hu", giving effect of hesitation before last note of each song; unique among New World *Glaucidium*.

Habitat. Subtropical evergreen forest at 1450-1975 m on Andean slopes; all known localities where species observed are on outlying ridges, so possibly restricted to such ridges; inhabits subcanopy.

Food and Feeding. Little known; probably large insects, small lizards and small birds.

Breeding. No information.

Movements. Probably resident.

Status and Conservation. Not globally threatened. CITES II. Considered uncommon; easily overlooked. Predicted that species' range will be found to be more extensive than currently known.

Bibliography. Anon. (1995h), Heidrich *et al.* (1995a), Howell & Robbins (1995), Robbins & Howell (1995), Stotz *et al.* (1996), Williams *et al.* (1996).

134. Amazonian Pygmy-owl*Glaucidium hardyi*

French: Chevêchette d'Amazonie

German: Amazonaszwergkauz

Spanish: Mochuelo Amazónico

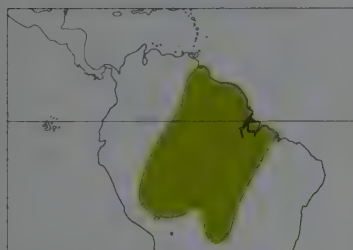
Other common names: Hardy's Pygmy-owl

Taxonomy. *Glaucidium hardyi* Vielliard, 1989, 20 km south-west of Presidente Medici, Rondônia, Brazil.

Considered member of *G. minutissimum* complex, which also includes *G. palmarum*, *G. sanchezi*, *G. griseiceps* and *G. parkeri*; traditionally considered race of *G. minutissimum*, but appears to differ in morphology, ecology and vocalizations; alternatively, considered more closely related to *G. jardini* and *G. bolivianum*; further study needed to determine true relationships. Monotypic.

Distribution. From SE Venezuela (Bolívar) E through the Guianas to N Brazil (Pará), and S to SE Peru, N & E Bolivia and S Mato Grosso.

Descriptive notes. c. 14 cm; c. 55-65 g. Tiny, with relatively small head and eyes and long wings, unmarked mantle and relatively dark, greyish rufous-brown plumage; dimorphic. Crown and nape brownish-grey with extensive white spotting, contrasting slightly with dark grey-brown back; nape with 2 black "false eye-spots", bordered by white; pale cinnamon spots on closed wings; 5 whitish bars on tail; sides of chest and streaking on underparts dusky cinnamon-brown; undertail with buffish bands. Rusty morph lacks light tail-bands. Differs from *G. parkeri* in much redder coloration and absence of bold white spots on wings; from *G. griseiceps* and *G. minutissimum* in paler and greyer head. Juvenile undescribed. **VOICE.** Rapid series of 12-36 notes running into quavering



roll or trill, at tempo of 10-13 notes per second but apparently varying across range; trill relatively loud and ringing, not analogous to the soft trills given by other members of *G. minutissimum* complex (which tend to give trill when agitated); female voice higher-pitched; frequently sings during day.

Habitat. Upper storey of humid evergreen rainforest, especially tall *terra firme*, transitional and *várzea* forest; forest edges and Amazonian lowlands; from sea-level to 850 m.

Food and Feeding. Mainly insects, probably also some small arboreal vertebrates, but little information.

Breeding. No information available.

Movements. No information. Probably resident.

Status and Conservation. Not globally threatened, CITES II. Generally considered uncommon, but may well be overlooked as it lives high up in forest; often kept as pet by native tribes. Vulnerable to forest destruction throughout range.

Bibliography. Bahr (1995), Heidrich *et al.* (1995a), Howell & Robbins (1995), Kirwan (1996a), König (1991b), O'Neill (1969), Olrog (1968), Parker & Remsen (1987), Pearson (1975), Robinson & Terborgh (1997), Sick (1993, 1997), Snyder (1966), Stotz, Fitzpatrick *et al.* (1996), Stotz, Lanyon *et al.* (1997), Tostain *et al.* (1992), Viellard (1989).

135. Least Pygmy-owl

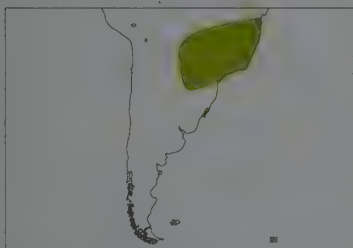
Glaucidium minutissimum

French: Chevêchette cabouré **German:** Kleinstzwerghauk **Spanish:** Mochuelo Mínimo
Other common names: Amazonian(!)/Brazilian Pygmy-owl

Taxonomy. *Strix minutissima* Wied, 1830, interior of the State of Bahia, Brazil.

Forms species complex with *G. palmarum*, *G. sanchezi*, *G. griseiceps*, *G. parkeri* and *G. hardyi*. All (except recently described *G. parkeri*) formerly treated as races of present species, but appear to have constant vocal differences; further research needed. Monotypic.

Distribution. E Paraguay, S & E Brazil and possibly NE Argentina (Misiones).



Descriptive notes. c. 14-15 cm. Very small; crown and nape dusky cinnamon-brown with whitish spots extending back to nape; prominent white-bordered black "eye-spots" on back of head; back rufous-brown; pale barring on wings; 5 pale bars on tail; rufous-brown to dark cinnamon-brown on chest sides, with streaks of same colour on flanks and belly; bill and cere greenish-yellow; iris and feet bright yellow. Distinguished from *G. gnoma* superspecies by smaller size and unmarked back; from *G. hardyi* by redder crown, upperparts and chest sides; from *G. parkeri* by paler, much redder plumage lacking bold white spots on scapulars

and wings; from *G. griseiceps* by more rufescent back and crown. Juvenile crown less heavily spotted, nape lacks "eye-spots". Southernmost populations palest and most rufous. **VOICE.** Song consists of series of double, low-pitched, long hoots, each separated by pause about equal to duration of note, and given in bouts that may last for long periods; also soft, quavering trill, sometimes repeated several times, usually prefacing hooting bouts; when excited, may utter up to 4 whistles; calls just before dawn, less often after dusk, only rarely during day.

Habitat. Tropical, humid evergreen forest canopy and edge to open bush canopy, from sea-level to 1100 m (mainly 500-800 m in SE Brazil).

Food and Feeding. Large insects, small lizards and small birds. Relatively short tail, similar to that of insectivorous *Micrathene whitneyi*, and fluttery, extremely manoeuvrable flight suggest less *Accipiter*-like hunting technique than *G. brasilianum* or *G. gnoma*, perhaps indicating larger proportion of insect prey in diet. Few data available indicate that species is both diurnal and nocturnal. Like other *Glaucidium*, hunts by perch-and-pounce technique.

Breeding. Little information. Presumed to breed in dry to early rainy season; nest in cavity in tree, probably most frequently woodpecker hole.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Possibly rare, though sometimes adopted as pet by native people; perhaps escapes attention because of less accessible, more forested habitat. Occurs at Estancia Itabo Private National Park, Paraguay. Habitat destruction probably represents a serious threat.

Bibliography. Allen (1995), Brooks *et al.* (1993), Dubs (1992), Forrester (1993), Hayes (1995), Heidrich *et al.* (1995a), Howell & Robbins (1995), Lowen *et al.* (1995), Olrog (1968), do Rosário (1996), Short (1975), Sick (1993, 1997), Stotz *et al.* (1996), Willis (1992).

136. Ferruginous Pygmy-owl

Glaucidium brasilianum

French: Chevêchette brune **German:** Brasilzwerghauk **Spanish:** Mochuelo Caburé

Taxonomy. *Strix brasiliana* J. F. Gmelin, 1788, Ceará, Brazil.

Considered by some authors to form superspecies with *G. tucumanum*, *G. peruanum* and *G. nanum*. Has been considered to include those as races, but recent studies have shown all to be vocally distinct and to differ in DNA. In past treated as conspecific with *G. jardinii*, but again differs in vocalizations and DNA. N populations (*cactorum*, *ridgwayi*, *saturatum*) recently proposed as forming separate species (*G. ridgwayi*); further study needed. Race *pallens* perhaps better placed in *G. tucumanum*. Twelve subspecies recognized.

Subspecies and Distribution.

G. b. cactorum van Rossem, 1937 - S Arizona S to SW Mexico.

G. b. saturatum Brodtkorb, 1941 - S Mexico (Chiapas) and Guatemala.

G. b. ridgwayi Sharpe, 1875 - S Texas through E & S Mexico to Panama.

G. b. medianum Todd, 1916 - N Colombia.

G. b. margaritae Phelps & Phelps, Jr., 1938 - Margarita I (Venezuela).

G. b. phalaenoides (Daudin, 1800) - N & E Venezuela, Trinidad and the Guianas.

G. b. duidae Chapman, 1929 - S Venezuela (Mt Duida).

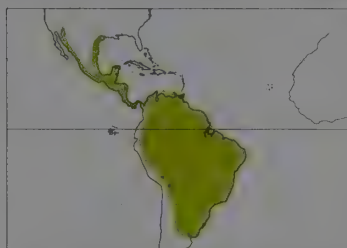
G. b. olivaceum Chapman, 1939 - SE Venezuela (Mt Auyan-Tepui).

G. b. ucayalae Chapman, 1929 - Amazonian Colombia, Venezuela and Brazil. S to S Peru and N Bolivia.

G. b. brasilianum (J. F. Gmelin, 1788) - NE Brazil S to NE Argentina and N Uruguay.

G. b. pallens Brodtkorb, 1938 - E Bolivia, W Paraguay and N Argentina.

G. b. stranecki König & Wink, 1995 - C Argentina to S Uruguay.



Descriptive notes. 15-19 cm; wingspan c. 38 cm; male 46-78 g, female 64-90 g. Long, narrow tail and distinctive whistled "popping" call. Very small; facial disc brown and rufous, flecked whitish; white eyebrows often fairly bold; crown, nape and upperparts grey-brown to rufous, crown and nape spotted buffish-white, nape with white-bordered black "false eyes"; tail with 5-8 light bars; eyes lemon-yellow, and bill, cere and toes greenish-yellow to greyish-yellow; legs feathered to talons. Polymorphic, with enormous variation in streaking: grey-brown morph has brown upperparts with cinnamon or cinnamon-buff spotting, upperpart-

coverts suffused cinnamon-rufous, and 7-8 rufous tail bands; grey morph differs in having greyish-brown upperparts and white tail bands; rufous morph (less common) entirely rufous, with no bars on tail. Rufous morph differs from that of *G. gnoma* in absence of tail bands and in less cinnamon-rufous upperparts; distinguished from *G. nanum* by smaller size, less bold white spotting on wing-coverts and scapulars, and shorter tail with fewer and broader bars. Juvenile similar to adult, but probably generally darker; crown and nape often greyer, with few or no pale spots on crown, "false eye-spots" indistinct or lacking, streaking below paler and more blurred. Races differ in size, in colour tone and in strength of markings: *stranecki* significantly larger; *ridgwayi* greyish, well spotted, streaks below shorter. **VOICE.** Advertising call a prolonged series of 10-60 whistling notes, c. 3 per second, sounding like "whoop" or "poip", usually with slight jerk of tail as each note uttered; female slightly higher, becoming a twitter; also chirping and ticking notes in alarm and other contexts; calls in daytime as well as at night, often attracting mobbing from small birds.

Habitat. Tropical lowlands and foothills in primary and secondary forest, coastal and thorn scrub, bushes and scrubby second growth, open and scattered woodland, riparian woodland, deciduous and gallery forest and forest edges, coffee plantations and suburban areas; also mesquite (*Prosopis*) woodland and xero-riparian habitats. Northernmost race *cactorum* occurs in saguaro (*Carnegiea*) desert habitats, in shady riparian timberland of mesquite groves, in cottonwood-mesquite habitats, in saguaro desert forest and dry riparian scrub along desert washes, in remnant woodland of mesquite, ebony (*Pithecellobium*) and cane along rivers. In Mexico, abundant in desert-like thorn scrub and thorn-forest zones, but absent from tropical deciduous forest and higher vegetational zones; from sea-level to 300 m in E, 1200 m in W. In Guatemala, ranges from scrubby woodland to edge of evergreen forest; in Belize and Honduras, occupies transitional areas between open pine savanna and rainforest, second-growth forest, and arid to semi-humid lowland habitat; in Panama, mainly tropical zone; to 1900 m in Central America and 2250 m in Venezuela. In S of range, *stranecki* found in open country with small groves or groups of trees and bushes, sometimes in parks and larger gardens; *pallens* in dry Chaco woodland.

Food and Feeding. Mostly insects; also reptiles, birds, mammals and amphibians; examples of prey items include grasshoppers (Acrididae), Tettigoniidae, scorpions, lizards (*Sceloporus*, *Phrynosoma*), mice (*Mus*, *Baiomys*, *Dipodomys*) and flycatchers (*Myiarchus*); in S Texas study, insects comprised 58% of diet, reptiles 22.5%, birds 10.5% and mammals 8.6%; mammals and amphibians made up less than 1% of prey deliveries; also observed taking prey larger than itself, such as hispid cotton rats (*Sigmodon*) and Eastern Meadowlarks (*Sturnella magna*); also recorded attacking captive guans (*Penelope*), eventually wearing out and killing them. Diurnal and crepuscular. Peak periods of prey deliveries to nest in early morning, midday and evening perhaps reflect prey behaviour and nutritional need: in early morning, passerines preoccupied with courtship and feeding, diurnal reptiles and insects emerge, small mammals become conspicuous, making them more susceptible to predation; at midday, reptiles and insects forage more to meet increased metabolic requirements, increasing availability; during evening, small mammals emerge in dim light, visual acuity of prey diminishes, and species must sustain brood through night. May also forage excessively in early morning and cache to meet mid-afternoon nutritional needs. Hunts mostly from perch; also by dashing into thick foliage to surprise prey.

Breeding. Lays generally c. Mar-Jun, during dry to early wet season; eggs found in S Mexico (Oaxaca) in Apr-May; breeding late Jan and Apr in Yucatán Peninsula; juveniles in Mar and July in NE Venezuela; probably lays in Oct in S of range. Probably monogamous, pair-bond lasting 1 year. Nest in natural cavity of tree, stump or snag, in woodpecker hole, tree fork or depression, trees used include mesquite, pine, cypress (*Cupressus*), palmetto (*Sabal*); no known records of nesting in saguaro; occasionally in hole in sand bank or termite mound; also known to use nestboxes, and in Argentina and Brazil old mud nest of Rufous Horned (Furnarius rufus). 2-5 eggs, usually 3 (average of 43 nests, 3-3); incubation 22-30 days; young hatch with eyes closed; female incubates and broods, male collects food for female and young, both adults brought prey to nest-site 3 weeks after young hatched; intense brood competition over prey items, occasionally resulting in fatal injuries to young; fledging 27-30 days, young cared for by both parents for at least 3 weeks more; young in captivity observed to return to nestbox to sleep. Sexual maturity at 1 year.

Movements. Resident, at least in N of range; no evidence of movements elsewhere.

Status and Conservation. Not globally threatened, CITES II. In USA, has declined drastically during 20th century; in Texas (lower Rio Grande valley), once generally distributed in riparian trees, brush, palm and mesquite thickets, now limited to remnant mesquite thickets and listed as threatened; in Arizona, has suffered from loss of preferred saguaro and associated riparian habitats and listed as endangered; future in USA uncertain. In Central and South America, considered widespread; fairly common to locally common in Panama and Colombia, and fairly common in Costa Rica; in some countries the only common pygmy-owl. Occurs in a considerable number of protected areas in most countries throughout its extensive range. In South America, this species (and other *Glaucidium*) kept as cage-birds in belief that they bring luck and success in love.

Bibliography. Anon. (1988), Baicich & Harrison (1997), Belton (1984), Binford (1989), Brooks *et al.* (1993), Canevari *et al.* (1991), Contreras *et al.* (1990), Eckert (1974), Fjeldså & Krabbe (1990), Friedmann (1948), Haverschmidt & Mees (1994), Heidrich *et al.* (1995a), Heintzelman (1992), Herklotz (1961), Hilty & Brown (1986), Howell & Webb (1995a), Johnson (1988), Johnson (1967), Kaufman (1996), König (1991b), König & Wink (1995), Land (1970), Lowery & Dalquest (1951), Marin *et al.* (1989), Meyer de Schauensee & Phelps (1978), Millsap & Johnson (1988), Monroe (1968), Olrog (1985), de la Peña (1994), Proudfoot & Beasom (1996, 1997), Proudfoot & Radomski (1997), Ridgely & Gwynne (1989), do Rosário (1996), Rowley (1984), Saibene *et al.* (1996), Schaldach (1963), Short (1975), Sick (1993, 1997), Slud (1964), Snyder (1966), Siles & Skutch (1989), Stotz *et al.* (1996), Tyler & Phillips (1978), Voous (1988), Wauer *et al.* (1993), Wetmore (1926, 1939, 1968a), Wolfe & de la Torre (1990), Zimmer (1930).

137. Tucuman Pygmy-owl

Glaucidium tucumanum

French: Chevêchette de Tucuman German: Tucumanzwergkauz Spanish: Mochuelo Tucumano

Taxonomy. *Glaucidium brasilianum tucumanum* Chapman, 1922, Rosario de Lerma, 4800 feet [c. 1600 m], Salta, Argentina.Considered by some authors to form superspecies with *G. brasilianum*, *G. peruanum* and *G. nanum*. Formerly treated as race of *G. brasilianum*, but differs in vocalizations and DNA. Race *pallens* of latter, with adjacent distribution and occupying similar habitat, perhaps better included with present species. Monotypic.**Distribution.** NW Argentina from Salta and Tucumán to at least Córdoba.**Descriptive notes.** 16-17.5 cm; c. 55 g. Dimorphic. Grey morph dark grey-brown to slaty-brown above, crown with very small, fine pale streaks, head sides and nape spotted, nape also with indication of "false eyes", back generally completely dark; wing-coverts and scapulars spotted light buffish-white; tail blackish-brown with 5-6 thin white bars; underparts whitish, darker on chest sides, streaked dark on flanks; iris and feet yellow; bill greyish-yellow. Rufous morph with fewer streaks and spots on head. Distinguished from *G. brasilianum* by darker upperside. Tends to become smaller and paler towards N of range.**VOICE.** Series of 10-30 or more equally spaced upward-inflected notes, c. 2 per second, becoming louder towards end; also single "wik" and chirping notes.**Habitat.** Semi-open, dry thorn forest: Chaco thorn-scrub and dry Chaco woodland. Generally up to c. 1500 m, locally to 1800 m.**Food and Feeding.** Little information; takes small birds, also other small vertebrates, and insects. **Breeding.** Males in breeding condition (enlarged testes) taken in Oct and Nov. Nest in old woodpecker hole in tree or cactus. 3-5 eggs; incubation by female, fed by male.**Movements.** Presumed resident.**Status and Conservation.** Not globally threatened. CITES II. Status uncertain, but probably not uncommon locally. Habitat destruction the main threat.**Bibliography.** Canevari *et al.* (1991), Chapman (1922), Friedmann (1927), Heidrich *et al.* (1995a), Stotz *et al.* (1996).

138. Peruvian Pygmy-owl

Glaucidium peruanum

French: Chevêchette du Pérou German: Peruzwergkauz Spanish: Mochuelo Peruano

Taxonomy. *Glaucidium peruanum* König, 1991, Ninabamba (2100 m), Apurímac, Peru. Considered to form superspecies with *G. brasilianum*, *G. tucumanum* and *G. nanum*. Recently separated from *G. brasilianum* based on bioacoustical analysis and DNA evidence. Even more recent research suggests that populations currently included in present species actually constitute two species, one on Pacific slope and the other on Amazonian slope; they differ markedly in morphology and, particularly, vocalizations; name *peruanum* is applicable to birds of Amazonian slope; scientific description of form from Pacific slope currently in preparation (see page 84). Probably constitutes two species, both apparently monotypic.**Distribution.** W Ecuador (Manabí) S through W Peru to N Chile; also E of Andes in extreme SE Ecuador (Zamora-Chinchi) and Marañón drainage of Peru.**Descriptive notes.** c. 15-17 cm; c. 60 g. Amazonian slope birds have quite large, rounded pale vinaceous-buff spots on crown, and conspicuous "face pattern" on nape, with large black patches, bordered below by almost continuous buff band. Very similar to *G. tucumanum*; best distinguished by voice. Sexually dimorphic in size, with male tiny. Juvenile has unspotted crown. Pacific slope birds have abundant pale streaks on crown, and poorly marked "face pattern" on nape; more fulvous in coloration, some markedly rufous. **VOICE.** On Amazonian slope birds song has a sharply declining pitch and speed. On Pacific slope, song is long

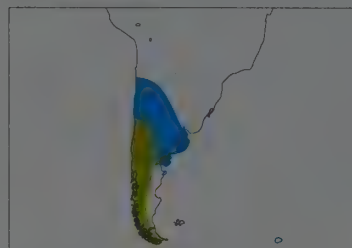
sequence of equally spaced notes in rapid succession (6-7 notes per second) on a constant pitch.

Habitat. Riparian woodland, thickets, semi-arid woodland, mesquite, and elfin forest; also agricultural country with trees, and locally urban parks. From lowlands and foothills to c. 3000 m.**Food and Feeding.** Insects and small birds known to be taken. Forages in middle storey and canopy; hunts from perch.**Breeding.** Nest situated in tree hole, often of woodpecker; no other information.**Movements.** Probably resident.**Status and Conservation.** Not globally threatened. CITES II. Generally considered rare, but probably relatively common locally; difficult to observe. Only recently described, and conservation status may require reassessment, but as two species are probably involved, taxonomic clarification is immediate priority; research required on both forms.**Bibliography.** Becker & López (1997), Best *et al.* (1996), Heidrich *et al.* (1995a), König (1991b), Parker *et al.* (1995), Pople *et al.* (1997), Stotz *et al.* (1996), Taylor (1995), Williams *et al.* (1996).

139. Austral Pygmy-owl

Glaucidium nanum

French: Chevêchette australe German: Araukanerkauz Spanish: Mochuelo Patagón

Taxonomy. *Strix nana* King, 1828, Port Famine, Straits of Magellan.Considered by some authors to form superspecies with *G. brasilianum*, *G. tucumanum* and *G. peruanum*. Sometimes treated as race of *G. brasilianum*, but apparently some subtle differences in vocalizations exist; recently shown to differ also in DNA. Monotypic.**Distribution.** Breeds S Chile and S Argentina S to Tierra del Fuego, some wintering farther N in Chile and Argentina.**Descriptive notes.** 17-22 cm; male 55-75 g, female 70-100 g. Dimorphic. Grey-brown morph grey-brown overall, with white spotting; crown minutely streaked white, and black "false eye-spots" on back of head; numerous white spots on wing-coverts and scapulars; tail with 7-10 distinct rufous or rarely white bars; densely streaked below. Rufous morph similar, but with rufous replacing grey-brown. Differs from *G. brasilianum* in larger size and darker general coloration; rufous morph less fox-red than in latter species; differs from *G. jardiinii* in having more numerous and rufous tail-bars, and streaked (not dotted) crown. Juvenile has uniform brown crown.**nape, mantle and chest. VOICE.** Series of 22-66 short whistles repeated in rapid succession, at about 3 whistles per second, each with upward inflection; also chirping and ticking notes.**Habitat.** Warm desert areas, oases and puna, warm shrubland, temperate forest, and cold forest of southern beech (*Nothofagus*) interspersed with steppe areas; also open woodland, thorn scrub, and sometimes city parks and gardens. Found in evergreen shrubland in C Chile and in humid forest in S Chile; in southernmost Chile, southern beech forest and Patagonian scrub. Occurs from sea-level to 2000 m in Chile, and to 1500 m in Patagonia (Argentina).**Food and Feeding.** Primarily birds, such as Plain-mantled Tit-spinetail (*Leptasthenura aegithaloides*), White-crested Elaenia (*Elaenia albiceps*), Common Dicaea-finch (*Dicaea dicaea*), Austral Blackbird (*Curaeus curaeus*), Moustached Turca (*Pteroptochos megapodius*), juvenile Chilean Tinamou (*Nothoprocta perdicaria*), Rock Dove (*Columba livia*) and domestic fowl; often takes prey considerably larger than itself, even twice its size; average prey weight 45% of owl's size. Other prey includes insects, reptiles, arachnids, small mammals and many nocturnal tenebrionid beetles; in NC Chile found to be better depicted as small-mammal eater that secondarily preys on birds, this probably reflecting mouse outbreak that occurred during study and suggesting that species is opportunistic. Most often described as nocturnal and diurnal, but in Patagonia observed as mostly crepuscular and diurnal. A perch-and-wait predator; will attack passerines in mist-nets; remains found under plucking sites indicate that only wing and tail feathers removed; caches surplus prey in rock crevices.**Breeding.** Lays in Sept-Nov (austral spring). Nest in hollowed tree trunk, tree crotch, rock bank, ground cavity, rodent burrow or building; also uses cavities of Dark-bellied Cinclodes (*Cinclodes patagonicus*), Chilean Flicker (*Colaptes pitius*) and Striped Woodpecker (*Picoides lignarius*); nest may be reused several times, but unclear whether by same pair; pairs generally nest c. 200 m or more apart, report of 2 pairs sharing same tree considered highly unlikely. Single clutch of 3-5 eggs; incubation period 26-28 days, report of 15-17 days (shortest incubation reported for any owl) requires corroboration.**Movements.** Partial migrant. Southernmost populations migrate N in late autumn to N Argentina (Buenos Aires, Santa Fe, Entre Ríos and Tucumán) and N Chile; population in Chile's southernmost Magallanes region resident.**Status and Conservation.** Not globally threatened. CITES II. In Chile, considered most abundant owl; common in C & S in summer, autumn and winter, and either leaves or becomes secretive in spring; appears to be increasing in C Chile, despite being killed by rural people because believed to be bird of ill omen. In Argentina, abundant in region S from Neuquén and Río Negro. Seems generally tolerant of human-induced habitat changes, and gardening may increase avian prey (passerine) abundance. Occurs in a number of protected areas, e.g. Tierra del Fuego National Park, where it can be fairly common and very tame.**Bibliography.** Canevari *et al.* (1991), Chebez & Bosso (1992), Ejelds & Krabbe (1990), Heidrich *et al.* (1995a), Hellmayr (1932), Humphrey *et al.* (1970), Jaksic *et al.* (1992), Jiménez & Jaksic (1989, 1993), Johnson (1967), König (1987, 1991b), Marin *et al.* (1989), Meyer de Schauensee (1966, 1982), Narosky & di Giacomo (1993), Nellar (1993), Norez *et al.* (1983), Olrog (1984), de la Peña, M.R. (1994, 1997), Stotz *et al.* (1996), Wetmore (1926).

140. Cuban Pygmy-owl

Glaucidium siju

French: Chevêchette de Cuba German: Kubakauz Spanish: Mochuelo Sijú

Taxonomy. *Noctua siju* d'Orbigny, 1839, Cuba.

Affinities uncertain. Two subspecies recognized.

Subspecies and Distribution.*G. s. siju* (d'Orbigny, 1839) - Cuba.*G. s. vittatum* Ridgway, 1914 - I of Pines.**Descriptive notes.** 16-17 cm; 55-90 g. Tiny; crown, head sides and back greyish-brown with white spots; eyebrows whitish to cinnamon; nape with white-edged dark "eye-spots", mantle barred; tail with 5-6 white bars; throat brown; breast sides and flanks brownish, barred darker, breast centre plain white, rest of underparts off-white with dark brown spots and streaks; bill, iris and tarsus yellow. Rufous morph also occurs. Juvenile with unspotted crown. Race *vittatum* larger, upperparts more clearly barred.**VOICE.** Whistle-like "jiu" at short intervals, or repeated "jiu, jiu, jiu, jiu", starting softly and increasing in frequency and tone.**Habitat.** Coastal, deciduous and montane forest, forest edges, second growth, and open areas with scattered trees and cultivated fields; locally, plantations and larger parks. From sea-level to 1500 m.**Food and Feeding.** Insects; also lizards, frogs, small mammals and birds. Hunts from perch.**Breeding.** Breeds in dry season. Lays in abandoned nest of other bird or in natural tree cavity; 3-4 eggs; incubation by female.**Movements.** Resident.**Status and Conservation.** Not globally threatened. CITES II. Considered fairly common to common, although little information on species' biology, and no conclusive comments can be made regarding status. Also, race *vittatum* has restricted distribution. Adversely affected by destruction of small patches of woodland; conservation problems the same as those that face island species generally.**Bibliography.** Allen (1961), Anon. (1998a), Barbour (1943), Bond (1985), Criado *et al.* (1995), Gundlach (1873), Heidrich *et al.* (1995a), Raffaele *et al.* (1998), Stotz *et al.* (1996), Sulley & Sulley (1992), Wotzkow (1990).



141. Red-chested Owlet

Glaucidium tephronotum

French: Chevêchette à pieds jaunes **German:** Rotbrustkauz **Spanish:** Mochuelo Pechirrojo
Other common names: Yellow-legged Owlet

Taxonomy. *Glaucidium tephronotum* Sharpe, 1875, South America; error = Mampong, Ashanti, Ghana.

Relationships uncertain. Proposed races *lukolelae* from CW Zaire and *kivuense* from E Zaire included within race *medje*. Four subspecies currently recognized.

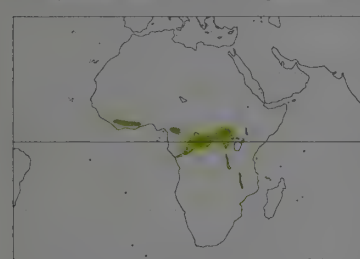
Subspecies and Distribution.

G. t. tephronotum Sharpe, 1875 - Liberia, Ivory Coast and Ghana.

G. t. pyrafrati Bates, 1911 - Cameroon.

G. t. medje Chapin, 1932 - Congo Basin, E Zaire and SW Uganda.

G. t. elongense Granvik, 1934 - E Uganda and W Kenya.



with pale spots on head sides, heavy spotting below, including breast sides. **Voice.** Series of 2-20 high whistles given at 2-second intervals, "teu, teu, teu, teu,..." or yelping "wook wook wook..."; sometimes double note, "wu wook, wu wook"; breaks of 2-5 seconds between series; female may give series of faster, higher whistling notes.

Habitat. Dense primary forest and forest-scrub mosaic; also recorded in logged forest. In lowlands and at up to 2150 m.

Food and Feeding. Varied; eats insects such as mantises, cockroaches, crickets, earwigs and cicadas; pursues moths and other winged insects in forest canopy; also some small mammals and birds. Mainly nocturnal, hunting in forest openings and edges. Reports of diurnal activity: recorded active on rainy afternoon, one observed flying at midday, another seen catching passerine in daylight, but usually roosts in cavities by day.

Breeding. Little known. In Liberia, a female with enlarged ovaries and having laid recently in late mar; in Ghana, a collected female finished laying in Feb. Nest in tree cavity or hollow; 2-4 eggs.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Rare and hard to locate. Nominate race rare to not uncommon in Liberia, e.g. Mt Nimba; race *elongense* uncommon in Kenya at Mt Elgon, N Nandi, Kakamega, Mau and Trans-Mara Forests; only 1 fully confirmed nesting record in Kenya. Species occurs in several protected areas, such as Impenetrable (Bwindi) Forest National Park, Uganda, and Mount Elgon National Park, Kenya. In Central African Republic, up to 4 singers heard from same station in exploited forest may suggest that species can be locally common and that it can tolerate some degree of habitat alteration.

Bibliography. Bannerman (1953), Bowden & Andrews (1994), Brown (1977), Christy & Clarke (1994), Colston & Curry-Lindahl (1986), Dowsett (1989b, 1990), Dowsett & Dowsett-Lemaire (1991, 1993), Dowsett & Forbes-Watson (1993), Dowsett *et al.* (1999), Field (1998), Fry *et al.* (1988), Gatter (1988, 1997), Grimes (1987), Kemp & Kemp (1998), Lewis & Pomeroy (1989), Lippens & Wille (1976), Louette (1981), Mackworth-Præd & Grant (1957, 1970), Short *et al.* (1990), Snow (1978), Thiollay (1985), Zimmerman, D.A. (1972), Zimmerman, D.A. *et al.* (1996).

142. Sjöstedt's Owlet

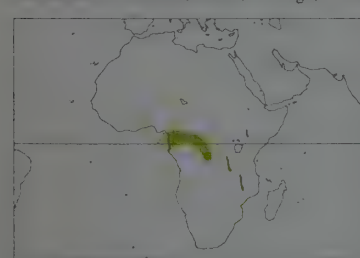
Glaucidium sjöstedti

French: Chevêchette à queue barrée **German:** Prachtkauz **Spanish:** Mochuelo del Congo
Other common names: Sjöstedt's Barred Owlet, Chestnut-backed Owlet(!)

Taxonomy. *Glaucidium sjöstedti* Reichenow, 1893, Mount Cameroon.

Affinities uncertain. Monotypic.

Distribution. Cameroon, Gabon, N Congo, S Central African Republic and NW & C Zaire.



accelerating notes that drop in pitch and volume at end, "kroo kroo krookrookrookroo"; calls mainly at dawn and dusk.

Habitat. Restricted to primary lowland forest, ascending somewhat higher on Mt Cameroon; avoids forest edge or damper places where vine-palm flourishes.

Food and Feeding. Mainly insects such as grasshoppers and dung beetles; also spiders, mice, small snakes, crabs and nestling birds; known to attack small birds caught in mist nets. Nocturnal hunter;

Descriptive notes. c. 20-25 cm; c. 140 g. Head and neck brown with white barring; facial disc brown with buff-white barring; eyes and bill yellow; distinct white throat and eyebrows; upper back barred brown and white, rest of upperparts deep chestnut; flight-feathers conspicuously barred brown and white; tail brown with thin white bars; underparts cinnamon, uniformly barred brown. Juvenile paler, with buffy underparts and chestnut wash across throat, faint dark barring on upper chest, also barred buff on scapulars. **Voice.** 2-4 notes uttered over 2 seconds, "kroo-kroo-kroo", with 1-second interval between series; sometimes male gives

sometimes mobbed by small birds if disturbed from daytime roost. Hunts in understorey, within 2 m of ground.

Breeding. Lays in Jul in Gabon; nestlings found in Cameroon in Feb, May, Aug, Nov and Dec. Nest in cavity or natural tree hollow c. 1-5 m above ground; based on spacing of calling males in Gabon, territory c. 10-12 ha, 2 nestlings collected once, so clutch size at least 2; incubation c. 28 days; fledging period unknown.

Movements. Probably resident, making only local movements.

Status and Conservation. Not globally threatened. CITES II. Uncommon in most of range; most frequent in Gabon, where locally not uncommon, e.g. at La Lopé Reserve. Some authors give status as uncertain, possibly endangered; habitat destruction almost certainly a threat. Much needs to be learned of species' breeding biology and distribution before accurate assessment of its status can be made.

Bibliography. Bannerman (1953), Bowden & Andrews (1994), Brosset & Éard (1986), Christy & Clarke (1994), Dowsett (1989a, 1989b), Dowsett & Dowsett-Lemaire (1991, 1993), Dowsett & Forbes-Watson (1993), Dowsett *et al.* (1999), Elgood *et al.* (1994), Fry *et al.* (1988), Kemp & Kemp (1998), Lippens & Wille (1976), Louette (1981), Mackworth-Præd & Grant (1970), Snow (1978).

143. Asian Barred Owlet

Glaucidium cuculoides

French: Chevêchette cuculoïde **German:** Kuckuckstrillerkauz **Spanish:** Mochuelo Cuco
Other common names: Barred Owlet, Cuckoo Owlet(!), Cuckoo Owl

Taxonomy. *Noctua cuculoides* Vigors, 1831, Simla-Almora district, Himalayas.

Possibly forms superspecies with *G. castanonotum*. Sometimes considered to include latter and *G. castanonotum* as races. Eight subspecies recognized.

Subspecies and Distribution.

G. c. cuculoides (Vigors, 1831) - Himalayas from NE Pakistan and Kashmir E to W Sikkim.

G. c. austerum Ripley, 1948 - E Sikkim, Bhutan, NE Assam and NW Myanmar.

G. c. rufescens Stuart Baker, 1926 - NE India, Bangladesh and N Myanmar.

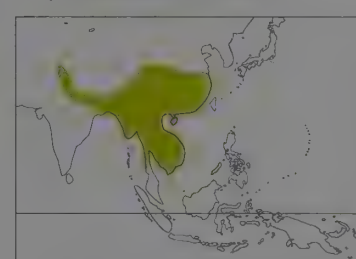
G. c. bruegeli (Parrot, 1908) - S Myanmar and S Thailand.

G. c. delacouri Ripley, 1948 - N Indochina.

G. c. deignani Ripley, 1948 - SE Thailand and S Indochina.

G. c. whiteleyi (Blyth, 1867) - W, C & SE China and NE Vietnam.

G. c. persimile Hartert, 1910 - Hainan.



Descriptive notes. 22-25 cm; 150-175 g, female slightly larger. Head grey-brown, barred buff, with whitish eyebrows; upperparts dark brown, barred buff to fulvous; scapulars edged buff-white, forming row of spots down sides of back; tail and wings dark brown, barred; below, white patches on throat and middle breast, rest of underparts barred dark and light; iris yellow; bill yellow-green, darker on cere; feet greyish-yellow or dull horn-green. Distinguished from *Athene brama* by barred instead of spotted upperparts; from *G. radiatum* by larger size and darker coloration. Juvenile has breast streaked, not barred, and is more rufous on crown and mantle. E races more rufous, with lower underparts and flanks broadly streaked rufous on white. **Voice.** Trill, lasting 7-14 seconds; series of squawks, rising to crescendo, then ending abruptly; during breeding season, more musical, bubbling whistle, "wowowowowowowow"; territorial song varied series of barking high notes; loud, clear "hooloo hooloo hooloo", broadening to violent "kok kok", ending with short, shrill "chiurr".

Habitat. Open forest of pine and oak, subtropical evergreen jungle, scrub; sometimes near human habitation. From lowland plains to 1800 m; to 2700 m in Himalayas of N Pakistan.

Food and Feeding. Mainly insects, including beetles and grasshoppers; also lizards, rodents, small birds and frogs. Mostly diurnal. Hunts from perch, with undulating flight; catches birds such as quail (*Coturnix*, *Perdula*) in air; insects caught in flight or on ground.

Breeding. Lays Apr-Jun in Nepal, Apr-May elsewhere; pair observed together throughout Mar-Aug; fledgling found early Jul. Nest in unlined tree cavity; may kill barbets (*Capitonidae*) and woodpeckers (*Picidae*) for cavity. 4 eggs (3-5); both sexes said to incubate and to feed young, requires confirmation.

Movements. Mainly resident. Makes elevational movements on S Himalayan slopes; may also make vertical movements in W Chinese mountains, descending to lowlands of Sichuan and river bottoms of W Hubei; possibly more extensive movements in NC China, where winter climate severe.

Status and Conservation. Not globally threatened. CITES II. Common over most of range. Tolerates human proximity; nests in fruit gardens near Bangkok, Thailand, and in coconut plantations; in China, occurs close to farmhouses and footpaths in rice fields.

Bibliography. Ali & Ripley (1981), Ali *et al.* (1996), Bangs & Van Tyne (1931), Cheng Tsohsin (1987), Deignan (1945), Dudgeon (1901), Étchécopar & Hue (1978), Grimmett *et al.* (1998), Inskipp, C. & Inskipp (1991), Inskipp, T. *et al.* (1996), Lekagul & Round (1991), Majumdar *et al.* (1992), Riley (1938), Ripley (1982), Roberts (1991), Smythies (1986), Stepanyan (1995), Voous (1988), Wells (1999), Zhao Zhengjie (1995).

144. Javan Owlet

Glaucidium castanonotum

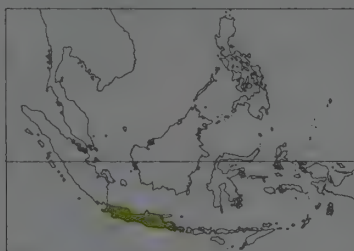
French: Chevêchette spadicee **German:** Trillerkauz **Spanish:** Mochuelo de Java
Other common names: Javan Barred/Chestnut-winged/Spadiced Owlet, Cuckoo Owlet(!)

Taxonomy. *Strix castanonotera* Horsfield, 1821, Java.

Possibly forms superspecies with *G. cuculoides*. Formerly treated as isolated race of latter. Monotypic.

Distribution. Java and Bali.

Descriptive notes. c. 24 cm. Indistinct facial disc barred rufous and orange-yellow, with white eyebrows; head brown with fine pale orange-yellow barring; upperparts rufous-chestnut, scapulars



edged with broken white line; wings and tail barred orange-yellow and brown; below, rufous breast sides barred orange, flanks and belly sides broadly streaked brownish-rufous; iris yellow-brown; bill greenish with yellow tip; feet greenish-yellow. Voice, Rapid trill, descending in pitch while increasing in volume; given at dawn and dusk.

Habitat. Primary and secondary forest, from lowlands to 900 m, locally higher, to 2000 m.

Food and Feeding. Insects, mice and small birds; occasionally reptiles. Mainly nocturnal, but sometimes active by day. Hunts from perch, pounces on prey.

Breeding. Probably similar to that of *G. cuculoides*; presumed to nest in woodpecker hole or other tree cavity; 4 eggs. No other information available.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Considered common locally in forest fragments and hills. Little information available; ecology and tolerance of human activities may be similar to those of *G. cuculoides*; detailed information much desired. Habitat loss probably main threat.

Bibliography. Andrew (1992), van Balen (1991), Hellebrekers & Hoogerwerf (1967), Hoogerwerf (1949a), Inskipp *et al.* (1996), MacKinnon (1988), MacKinnon & Phillips (1993), Mees (1971), Voous (1988).

145. Jungle Owlet

Glaucidium radiatum

French: Chevêchette de jungle **German:** Dschungelkauz **Spanish:** Mochuelo de Jungla
Other common names: Barred Jungle Owlet

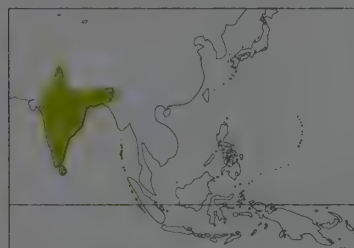
Taxonomy. *Strix Radiata* Tickell, 1833, jungles of Borahum and Dholbhum.

Possibly forms superspecies with *G. castanonotum*, with which has been considered conspecific; although both present in Sri Lanka, they occupy different habitats. Two subspecies recognized.

Subspecies and Distribution.

G. r. radiatum (Tickell, 1833) - Himalayas from Himachal Pradesh E to Bhutan, Bangladesh and possibly W Myanmar, and S through India; also Sri Lanka.

G. r. malabaricum (Blyth, 1846) - SW India.



Descriptive notes. 20-24 cm; 90-114 g. Small, squat, round-headed owl. Facial disc barred brown and cream, with distinct white eyebrows, chin and moustachial streak; dark brown above, wings more rufous, all barred uniformly with pale rufous; below, barred dark olive-brown and white; rufous patch on underwing conspicuous in flight; iris bright yellow; bill greenish-white; feet greenish-yellow. Differs from *G. cuculoides* in smaller size, paler general appearance and rufous primaries. Juvenile undescribed. Race *malabaricum* much darker, more rufous overall.

VOICE. Long, monotonous, musical "cur-cur-

cur-cur-ur", fading towards end; uttered for up to 15 minutes at a time; also "kao" repeated 2-3 times, followed by quickening series of fading double notes, resembles Red Junglefowl (*Gallus gallus*).

Habitat. Both dense and sparse deciduous forest, scrub, *terai* and dun in Nepal; sometimes near cultivation; also secondary growth from cleared forest; avoids wet forest. From lowlands to 915 m in Nepal; up to 2000 m in rest of range.

Food and Feeding. Mostly insects, including beetles, locusts, grasshoppers and cicadas; also lizards, rodents and small birds. Largely crepuscular; most active hour before dusk and hour after sunrise. Flight swift and direct, similar to small hawk (*Accipiter*).

Breeding. Mar-Jun in Nepal, Mar-May elsewhere. Nest in unlined tree cavity, 3-8 m above ground. Usually 3 eggs (2-4); in Sri Lanka, only 2.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Status poorly known. Common in Nepal and India; common in Sri Lanka, but suffering under deforestation. Occurs in several protected areas such as Chitwan National Park, Nepal, Corbett and Periyar National Parks, India, and Yala National Park, Sri Lanka. Attempts at captive breeding unsuccessful: copulation occurred but no eggs laid.

Bibliography. Ali (1996), Ali & Ripley (1981), Daniels (1997), Gokula & Vijayan (1997), Grimmett *et al.* (1998), Henry (1998), Inskipp, C. & Inskipp (1991), Inskipp, T. *et al.* (1996), Lamsfuss (1998), Majumdar *et al.* (1992), Mohan (1997), Neelakantan (1971), Phillips (1978), Ripley (1982), Saha & Dasgupta (1992), Smythies (1986).

146. Chestnut-backed Owlet

Glaucidium castanonotum

French: Chevêchette à dos marron **German:** Kastanienmantelkauz **Spanish:** Mochuelo de Ceilán
Other common names: Sri Lanka Chestnut-backed Owlet

Taxonomy. *Athene castanonota* Blyth, 1852, Sri Lanka.

Possibly forms superspecies with *G. radiatum*; although both present in Sri Lanka, they occupy different habitats. Formerly treated as race of either *G. cuculoides* or *G. radiatum*. Monotypic.

Distribution. Sri Lanka.

Descriptive notes. 19 cm. Small owl, similar in shape and size to *G. radiatum*. Differs from latter in darker and greyer head; entire upperparts barred chestnut and blackish; and underparts white, barred dark on breast and flanks, but streaked olive-brown on belly. Juvenile undescribed. Voice, Far-carrying "krraw krraw krraw": calls during day.

Habitat. Dense forest of wet zone, from lowlands to 1950 m. Has been recorded at edge of rubber plantation. Frequents tops of tall trees, usually on steep hillsides.

Food and Feeding. Mostly insects; also mice, lizards and small birds; takes larger prey primarily when young being fed. Often hunts in daytime.



Bibliography. Ali (1996), Ali & Ripley (1981), Grimmett *et al.* (1998), Henry (1998), Hoffmann (1998), Inskipp *et al.* (1996), Kotagama & Fernando (1994), Lamsfuss (1998), Phillips (1978), Ripley (1982), Stattersfield *et al.* (1998), Wijesinghe (1994).

147. African Barred Owlet

Glaucidium capense

French: Chevêchette du Cap **German:** Kapkauz **Spanish:** Mochuelo de El Cabo
Other common names: Barred Owl(!), Ngami Owlet (*ngamiense*); Scheffler's Owlet, Eastern Barred Owlet (*scheffleri*)

Taxonomy. *Noctua Capensis* A. Smith, 1834, 17 km west of Bathurst, eastern Cape Province.

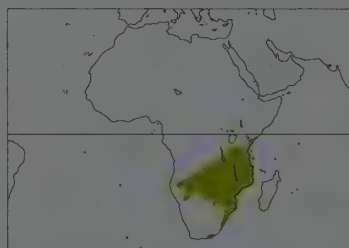
Has been suggested as forming superspecies with *G. castaneum* and *G. albertinum*. Some authors have considered present species conspecific with *G. castaneum*, or, alternatively, to include only disjunct W African race *etcheopari* of that species. Recent studies have indicated that *ngamiense* (including intergrade forms "*clanceyi*" and "*robertsi*") and *scheffleri* should both be regarded as distinct species, on basis of morphology, geographical distribution, habitat preferences and slight vocal differences, but more research needed. Three subspecies recognized.

Subspecies and Distribution.

G. c. scheffleri Neumann, 1911 - extreme S Somalia and E Kenya to NE Tanzania.

G. c. ngamiense (Roberts, 1932) - C Tanzania and SE Zaire across to S Angola, S to N Namibia, N Botswana, E Transvaal and SC Mozambique; also Mafia I.

G. c. capense (A. Smith, 1834) - from S Mozambique S to E Cape.



Descriptive notes. c. 20-22 cm; wingspan c. 45 cm; male 83-132 g, female 93-139 g; male 93-100 g, female 95-113 g (*scheffleri*). Small owl with large, round head. Head and nape grey-brown with fine white spots; facial disc white with light grey bars; upperparts brown, barred paler; scapulars and wing-coverts with broad white edges; flight-feathers brown with broad rufous bands; tail similarly banded; upper breast cinnamon, barred buff; lower breast and belly white with large brown feather tips, giving spotted appearance; eyes yellow, bill greenish-yellow. Juvenile browner on head and neck, with less barring and spotting on breast.

Race *ngamiense* smaller than nominate, head brown with white bars (not fine white spots), facial disc with broad white bars, upperparts light brown with distinct narrow buff bars, tail bands broader, belly with smaller dark spots; *scheffleri* has brown head evenly spotted white, facial disc with faint greyish barring, more prominent white eyebrows, darker brown upperparts with less barring, upper breast creamy-white with rusty-brown bars, and juvenile resembles adult. Voice, Nominative race gives 5-8 notes at 1 per second, rising in pitch and falling slightly with third note, "cow, cow, cow..."; sequence repeated 15-20 seconds later. Race *ngamiense* gives series of 6-10 low, whistled notes with half-second intervals between; may rise and fall in volume; also series of 35-55 fast purring trills; calls mainly at night. Race *scheffleri* utters 6-10 loud notes that increase and decrease in volume, "kerr-kerr-kerr-KERR-KERR-kerr", often followed by purring whistle; also repeats monotonous single note, "weu-weu-weu-weu...".

Habitat. Woodland and riparian trees in open country, usually below 1200 m; *ngamiense* inhabits lowland and montane forest and dense secondary growth; *scheffleri* coastal forest and woodland, again mainly below 1200 m.

Food and Feeding. Insects such as beetles, grasshoppers and caterpillars; small mammals and birds. Most details recorded for *ngamiense*; mainly insectivorous, also taking scorpions and occasionally small birds and amphibians such as skinks and frogs; preference for small prey may be due to weak feet (smaller than those of *G. perlatus*). Presence of leaf litter to support ground insects may limit distribution. Active during day, often hunting at dusk and early morning, but more nocturnal than *G. perlatus*; frequently mobbed by passerines; bathes regularly. Hunts by searching ground from perch, and dropping to catch prey. Like congeners, flies low and fast with dipping woodpecker-like flight, but does not flick tail back and forth when excited. Race *scheffleri* also recorded taking small reptiles and probably arthropods; perches in fairly open sites during day; mainly diurnal but also nocturnal; most active at dusk and early morning.

Breeding. Little information. Lays Sept-Nov in E & S Africa. Only few nests found, none studied in detail, and much of biology unknown: nest in cavity 3-6 m above ground; 2-3 eggs; both parents may feed young, which fledge at c. 32 days.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Nominative race very rare in E Cape, where first specimen collected in 1824, with another in 1826; speculation that locality may have been mislabelled or, if correct, owl extinct; rediscovered in 1980, when one found dead next to house in Kenton-on-Sea; in Aug 1981 one photographed during daytime at Hluleka Nature Reserve on Transkei coast. Threatened by habitat destruction, bush clearance for agriculture occurring at alarming rate; especially dangerous to survival since ecology and exact habitat affinities so poorly understood. Race *ngamiense* localized but common in parts of range; reported as common at Moremi Wildlife Reserve in Botswana, and also in riparian forest along Okavango R in Caprivi Strip, Namibia. Race *scheffleri* uncommon; scattered inland records from Kondoa, Mombasa, Itala and Kibwezi; rare in N Tanzania; few records from S Somalia, where status uncertain but possibly commoner than the handful of records imply.

Bibliography. Alexander (1997), Anon. (1985b), Ash & Miskell (1998), Benson & Benson (1977), Benson *et al.* (1971), Brooke (1984), Brooke *et al.* (1983), Carlyon (1985), Carlyon & Meakin (1985), Dowsett & Dowsett-

Lemaire (1993), Dowsett & Forbes-Watson (1993), Fanshawe & Ngala (1994), Fry *et al.* (1988), Ginn *et al.* (1989), Harrison *et al.* (1997), Kemp & Calburn (1987), Kemp & Kemp (1998), Lewis & Pomeroy (1989), Lippens & Wille (1976), Mackworth-Praed & Grant (1957, 1962, 1970), Maclean (1993), Malherbe (1996), Penry (1994), Pickford *et al.* (1989), Pinto (1983), Prigogine (1983, 1985b), Short *et al.* (1990), Snow (1978), Steyn (1979, 1982, 1984, 1994b), Vincent (1990), Zimmerman, D.A. *et al.* (1996).

148. Chestnut Owlet

Glaucidium castaneum

French: Chevêchette châtaine **German:** Kastanienkauz **Spanish:** Mochuelo Castaño
Other common names: Chestnut Barred Owlet; Lake District/Ituri Owlet (*castaneum*)

Taxonomy. *Glaucidium castaneum* Neumann, 1893, Andundi, Zaire.
Has been suggested as forming superspecies with *G. capense* and *G. albertinum*. Has been treated as conspecific with *G. capense*; or sometimes disjunct race *etcheopari* alone placed with latter or even treated as separate species on grounds of distribution and ecology. Two subspecies recognized.

Subspecies and Distribution.

G. c. etcheopari Éard & Roux, 1983 - patchily in Liberia and Ivory Coast.

G. c. castaneum Neumann, 1893 - NE Zaire (Semliki Valley) and SW Uganda (Bwamba Forest).



Descriptive notes. 20-22 cm; c. 100 g. Pale facial disc with few darker rings, white eye-brows; head dark brown, densely spotted buffish; upperparts dark chestnut-rufous, scapulars and lesser wing-coverts with broad white edges; flight-feathers barred buff, 9-10 pale bars on tail; upper chest white with brown barring; belly with numerous dark spots; yellow eyes and bill. Differs from *G. albertinum* in usually more white on scapulars and wing-coverts. Juvenile undescribed. Race *etcheopari* smaller, upperparts dark with paler bars. **Voice.** Series of whistled "kyurr-kyurr-kyurr" notes, accelerating at end.

Habitat. Humid lowland, transitional and montane forest, at 1000-1700 m above sea-level; in W Africa (*etcheopari*), not uncommon in old secondary forest and even heavily logged forest.

Food and Feeding. Small vertebrates and large insects. Hunts mostly from perch.

Breeding. No information.

Movements. Probably resident.

Status and Conservation. Not globally threatened. CITES II. Status of nominate race uncertain. W African population isolated; considered uncommon to locally not uncommon in Liberia, and widespread and common in Ivory Coast; likely to occur in Ghana, requires investigation.

Bibliography. Brown (1977), Colston & Curry-Lindahl (1986), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Dowsett-Lemaire & Dowsett (1998a), Éard & Roux (1983), Fry *et al.* (1988), Gatter

(1988, 1997), Grimes (1987), Kemp & Kemp (1998), Lippens & Wille (1976), Mackworth-Praed & Grant (1970), Morel & Chappuis (1992), Prigogine (1983), Snow (1978), Thiollay (1985).

149. Albertine Owlet

Glaucidium albertinum

French: Chevêchette du Graben **German:** Albertseekauz **Spanish:** Mochuelo del Alberto
Other common names: Prigogine's Owlet

Taxonomy. *Glaucidium albertinum* Prigogine, 1983, Musangakye, Zaire.

Has been suggested as forming superspecies with *G. capense* and *G. castaneum*. Monotypic.

Distribution. Albertine Rift in E Zaire and N Rwanda.



Descriptive notes. c. 20 cm; female 73 g. Upperparts maroon-brown; forehead and nape with cream spots, leading to cream bars on upper mantle; scapulars with beige edges; back and uppertail-coverts unmarked; flight-feathers brown with pale brown bars; dark tail with c. 7 narrow cream bands; upper chest maroon-brown with broad cream bars, rest of underparts white with maroon-brown spots. Differs from *G. capense* in distinctly spotted head, plain back; and from *G. castaneum* in less white on scapulars and wing-coverts. Juvenile undescribed. **Voice.** No information.

Habitat. Montane forest, from c. 1000 m to 1700 m.

Food and Feeding. Stomach of 1 bird contained a beetle and a grasshopper.

Breeding. No information.

Movements. Unknown; probably resident.

Status and Conservation. VULNERABLE. CITES II. Restricted-range species; present in Albertine Rift Mountains EBA. Surviving numbers not known, but small number of specimens collected from an area well explored by ornithologists suggests that it is rare. Known from 5 specimens: 2 collected at Lundulu in E Zaire, and 1 each from Nyungwe Forest in Rwanda, Musangakye and Munga in Itombwe Mts. Presumably declining as result of forest clearance. Mountain forest W of L Edward and Nyungwe Forest in Rwanda have both been reduced in size. Kamituga has become an important mining centre, and possibility of clearance and economic exploitation in Itombwe Mts could become a major threat. Forest conservation plans have been prepared to protect mountains W of L Edward and Nyungwe Forest, although whether local authorities will implement them is uncertain.

Bibliography. Bennun & Njoroge (1996), Catterall (1992), Clark & Mikkola (1989), Collar & Andrew (1988), Collar & Stuart (1985, 1988b), Collar *et al.* (1994), Dowsett (1990), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Fry *et al.* (1988), Kemp & Kemp (1998), Prigogine (1953, 1971, 1983, 1985b), Schouteden (1950, 1954b), Snow (1978), Stattersfield *et al.* (1998), Vuilleumier *et al.* (1992).

150



151



ssp noctua



ssp vidalii



152



ssp lilith

ssp glaux



153



ssp indica

ssp brama



154



ssp punensis



155



ssp grallaria

ssp cunicularia



156



ssp magnus

ssp funereus



159



ssp iheringi

ssp harrisii



158



ssp brooksi

157



ssp acadicus

ssp richardsoni



PLATE 17

inches 5
cm 13

Genus *XENOGLAUX* O'Neill and Graves, 1977

150. Long-whiskered Owlet

Xenoglaux loweryi

French: Chevêchette nimbée German: Peruanerkauz Spanish: Mochuelo Peludo

Taxonomy. *Xenoglaux loweryi* O'Neill and Graves, 1977, 10 km northeast of Abra Patricia (1890 m), Departamento San Martín, Peru. Relationships unclear. Monotypic.

Distribution. N Peru (Río Mayo valley, NW San Martín).



Descriptive notes. 13-14 cm; one male 47 g, two females 46 g and 51 g. Distinctive, tiny, very short-tailed owl. Unique long "whiskers" around base of bill and on sides of facial disc, extending well beyond edge of face; plumage mainly warm brown, with few whitish spots above, short white eyebeams; belly with numerous thin whitish vermiculations; eyes orange-brown, bill greyish with yellow tip; tarsus and toes bare, pinkish. Juvenile undescribed. **VOICE.** No definite information; recent records suggest song possibly short, mellow whistles followed by faster, higher notes.

Habitat. Humid cloudforest with epiphytes and dense undergrowth, at c. 1900-2200 m.

Food and Feeding. Presumably insects. Apparently active at dusk.

Breeding. No information.

Movements. No information. Presumably resident.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Andean Ridge-top Forests EBA. Currently considered Near-threatened. Perhaps not uncommon within restricted range; no data on current numbers, which assumed to be small. Only 3 specimens known. Major threat comes from habitat loss; forest destruction in restricted area in which species found appears to be continuing. With nothing known about this owl's ecology and biology, conservation measures difficult to determine; much further research needed.

Bibliography. Anon. (1977), Cardiff & Rensen (1994), Clark & Mikkola (1989), Collar *et al.* (1992), Davies *et al.* (1994, 1997), Fjeldså & Krabbe (1990), O'Neill & Graves (1977), Parker *et al.* (1982), Shuker (1993), Stattersfield *et al.* (1998), Stephens & Traylor (1983), Stotz *et al.* (1996), Wege & Long (1995).

Genus *MICRATHENE* Coues, 1866

151. Elf Owl

Micrathene whitneyi

French: Chevêchette des saguaros German: Elfenkauz Spanish: Mochuelo de los Saguaros

Taxonomy. *Athene whitneyi* Cooper, 1861, Fort Mojave, Arizona.

Relationships unclear. Races *whitneyi* and *sanfordi* appear to intergrade in NW Mexico and S Arizona. Four subspecies recognized.

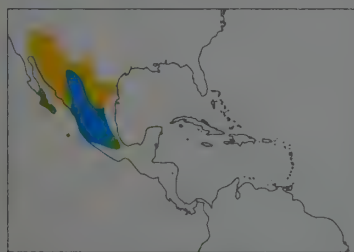
Subspecies and Distribution.

M. w. whitneyi (Cooper, 1861) - breeds SW USA (extreme S Nevada, SE California, C Arizona, SW New Mexico and SW Texas) S to NW Mexico (Sonora).

M. w. idonea (Ridgway, 1914) - S Texas S to C Mexico (S to Puebla, W to Guanajuato).

M. w. sanfordi (Ridgway, 1914) - S Baja California and parts of Mexican mainland.

M. w. graysoni Ridgway, 1886 - Revillagigedo Is (Socorro I).



Descriptive notes. 13-14 cm; 41 g. Distinctively small. Face and throat cinnamon to cinnamon-buff, supercilia white with narrow black tips; upperparts brownish-grey to greyish-brown with distinct buff or pale tawny spotting, spots bigger and somewhat darker on forehead; lower hindneck with narrow white collar; outer webs of scapulars mostly white, margined terminally with black; flight-feathers and wing-coverts spotted; tail with usually 4-5 pale brown-buff or buff-white bands; underparts mixed white, grey and dull pale cinnamon or buffy-brown; bill and legs pale horn; eyes lemon-yellow. Distinguished from

Glaucidium brasilianum by shorter tail, rufous-brown upperparts, and inactivity during daylight hours. Juvenile has crown deep brownish-grey, lacks warm cinnamon-buff tone on face or throat, underparts lack buff-brown and are marbled or clouded white and light brownish-grey and barred dark brown. Race *idonea* greyer above; *sanfordi* darker below; *graysoni* tinged olive above, with more cinnamon below and on tail. **VOICE.** High-pitched calls, 5-15 or more, reminiscent of yelping puppy; may be repeated for long periods (male advertisement).

Habitat. Cactus desert, riparian woodland, dry oak woodland, wooded canyons, mesquite; most abundant and widespread in riparian broadleaf forest. In SC Arizona, shows wide habitat tolerance, occurring in nearly all plant communities with arborescent vegetation, at up to 2000 m elevation;

elsewhere in SW USA, mainly in wooded or forested riparian corridors and adjacent arid hillsides, below 1900 m.

Food and Feeding. Entirely arthropods, primarily insects. In Arizona, noctuid moths and crickets (Orthoptera) dominated diet until summer rains, when beetles (*Phyllophaga*) became primary food; scorpions (*Jevois*) also important prey there, eaten after stingers removed; arachnids may be significant component of food of nestlings, perhaps comprising as much as half of total; diet varies seasonally with changes in insect availability. Obtains sufficient water from prey. Mainly crepuscular, with some nocturnal foraging. Hunts by flying over open ground, hovering above ground and capturing prey as they take flight; also pursues prey on ground, or hawks flying insects, making capture with feet. **Breeding.** Season May-Jun in USA, Mar-Aug in Mexico. Pair formation begins as soon as female arrives back; little known of bonding patterns or pair-forming behaviour. Nest almost exclusively in cavity excavated by woodpecker, such as Acorn and Gila Woodpeckers (*Melanerpes formicivorus*, *M. uropygialis*) and flickers (*Colaptes auratus*, *C. chrysoides*), in various trees and cacti, including sycamore (*Platanus*), cottonwood (*Populus*), walnut (*Juglans*) and saguaro (*Carnegiea gigantea*); frequently selects cavity in dead branches; cavity apparently offers some refuge from high temperatures, particularly in deserts. 1-5 eggs; incubation 21-24 days; first 2 eggs usually hatch about same time and third a day later, suggesting that incubation normally begins with laying of second egg; female incubates and broods; male feeds female, who passes food to young; fledging period 28-33 days; young apparently able to capture insects, such as crickets, as soon as they can fly. In Arizona, of average clutch size 2-6 eggs, 1-9 eggs hatched and 1-8 young fledged. First breeding at c. 1 year. **Movements.** N populations migratory, leave by mid Oct, winter in N & C Mexico in areas with abundance of insects and other arthropods; males precede females on spring migration, arriving in breeding areas from mid Feb to Apr. Resident in Baja California and on Socorro I.

Status and Conservation. Not globally threatened. CITES II. In Mexico, fairly common to common, but local; no indication of numbers. Almost extirpated in California, where classed as endangered by California Department of Fish and Game; however, species not included on federal or state lists of endangered and threatened species, nor under review for such listing. In California, desert habitat heavily damaged by damming of Colorado R and subsequent agricultural development, with disappearance of many old trees and cacti in which birds nested; by 1978, estimated 10 pairs remained in desert. Attempt has been made to replace lost habitat by planting native sycamores, cottonwoods and mesquite along new banks of Colorado R; also, in 1983-87 owl project, 13 individuals bred in captivity and total of 21 released into California; population in 1987 probably did not exceed 25 pairs. Considerable decline along Rio Grande valley in S Texas since late 19th century, although in SW Texas range expanding N. In Arizona, populations around metropolitan areas have probably decreased. In general, these distributional changes reflect human-induced loss of habitat, compounded in Texas by long-term climatic changes. Species may become endangered throughout US range in near future because riparian forest rapidly declining in SW as result of overgrazing, flood scouring, dewatering and streamflow regulation; clearance of riparian woodland for agriculture and homes particularly extensive in SE Texas. Population depends directly on availability of insect prey and woodpecker nest holes; competition for cavities with Common Starlings (*Sturnus vulgaris*) may negatively affect some populations. Research and management recommendations include surveys to locate additional breeding areas; developing a co-ordinated programme to monitor populations; acquiring conservation easements or obtaining landowner conservation agreements for Colorado R and Rio Grande Basin and restoring riparian forest along these rivers; maintaining riparian woodland in W Arizona drainage areas; maintaining instream flow, regulating or excluding livestock grazing and timber cutting, and seasonally closing sensitive areas to public access; and incorporating natural landscaping in housing developments in Arizona.

Bibliography. Anon. (1987), Baicich & Harrison (1997), Cardiff (1980), DeGraaf & Rappole (1995), Eckert (1974), Ely & Crossin (1972), Goad (1985), Goad & Mannan (1987), Halterman *et al.* (1987, 1989), Heintzelman (1992), Howell & Webb (1995a), Johnsgard (1988), Kaufman (1996), Manning & Goetze (1991), Millsap (1988), Phillips (1942), Small (1994), Stacey *et al.* (1983), Stotz *et al.* (1996), Tyler & Phillips (1978), Voous (1988), Walker (1993), Walters (1981, 1983), Wolfe & de la Torre (1990).

Genus *ATHENE* Boie, 1822

152. Little Owl

Athene noctua

French: Chevêche d'Athéna German: Steinkauz Spanish: Mochuelo Europeo

Taxonomy. *Strix noctua* Scopoli, 1769, Krain, Carniola.

Probably forms subspecies with *A. brama*. Race *lilith* shown in recent studies to differ in DNA and vocal patterns, may be separate species. Many races considered probably intermediate populations or reflection of individual variation, while geographical subspecific boundaries obscure, with intergrading populations: *vidalii* and *indigena* intergrade over wide area in NW Russia; *noctua* intergrades with *vidalii* over wide area from S France E to Czech and Slovak Republics and with *indigena* in former Yugoslavia; *indigena* and *vidalii* intergrade in N Ukraine, Belarus and C Russia; *lilith* intergrades with *saharae* in Saudi Arabia and with *bactriana* in Iraq, Corsican and Sardinian birds perhaps warrant subspecific status (as *sarda*). Proposed races *kesleri* and *caucasica* synonymous with *indigena*; *solitudinis* synonymous with *saharae*. Thirteen subspecies recognized.

Subspecies and Distribution.

A. n. vidalii A. E. Brehm, 1857 - W & N Europe (S Baltic S to Iberia, including Balearic Is) E to NW Russia.

A. n. noctua (Scopoli, 1769) - C Europe (from about S Germany) S to Sardinia and Sicily, E to Romania.

A. n. indigena C. L. Brehm, 1855 - Albania, SE Yugoslavia, S & E Romania, S Ukraine, S Russia, Caucasus and SW Siberia, S to Crete, Turkey (except SE) and Middle East (S to Haifa).

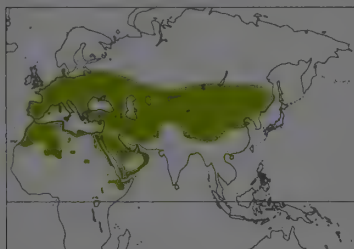
A. n. glaux (Savigny, 1809) - N Africa, and coastal Israel S from Haifa.

A. n. saharae (Kleinschmidt, 1909) - N & C Sahara (S to Mauritania, Mali, Niger, Chad and Sudan). E discontinuously into Arabian Peninsula.

A. n. spilogastra (Heuglin, 1869) - E Sudan, N Ethiopia.

A. n. somaliensis Reichenow, 1905 - E Ethiopia, Somalia.

A. n. lilith Hartert, 1913 - Cyprus, and inland Middle East from SE Turkey S to S Sinai.
A. n. bactriana Blyth, 1847 - from SE Azerbaijan, E Iraq, Iran and Afghanistan E through C Asia to L Balkhash.
A. n. orientalis Severetzov, 1873 - extreme NW China and adjacent Siberia.
A. n. impasta Bangs & J. L. Peters, 1928 - Kokonor, W Gansu.
A. n. ludlowi Stuart Baker, 1926 - SC China and S & E Tibet, S to N Himalayas.
A. n. plumipes Swinhoe, 1870 - NE China, Mongolia and Ussuriland.
 Introduced (*vidalii*), just outside natural range, to Britain; also introduced (*vidalii*) to New Zealand.



Descriptive notes. 21-23 cm; wingspan 54-58 cm; male c. 162-177 g, female c. 166-206 g (*vidalii*). Compact, plump and relatively small, with wings broad and rounded; flight undulating, with alternating bouts of flapping and closing wings. Plumage colour variable, from grey-brown or rufous-brown to ochre-buff; upperparts spotted white, underparts splashed; facial disc obvious on dark birds; eyes bright yellow; bill pale yellow; legs proportionately long, feathered, pale yellowish to white. Distinguished from *A. brama* by slightly larger size, absence of bold barring on underparts; from *Glaucidium passerinum*, *Aegolius*

funereus and smaller *Otus* species by more boldly spotted appearance, lack of ear-tufts or sharp corners to head, and distinctive calls and flight. Juvenile distinctly paler and much more uniformly patterned than adult; spots buff, not white, and streaking narrower and paler brown. Races differentiated by colour and size: *vidalii* darkest, dark umber-brown above with white flecking on crown and white spotting on mantle, scapulars and larger wing-coverts, sepia flight-feathers, ground colour of underparts white but with black-brown band across throat and broad dark brown splashing and streaking on lower breast and body, better-marked facial disc with white on edges of crown, around outer cheeks and under bill and eyes, but dusky from bill through eye and in half-circle in centre of cheeks; *lilith* palest, pattern similar to *vidalii* but with pale buff upperparts and extensive white markings; other races intermediate. Voice. Male advertising call a mellow hoot, "goook", rising sharply in pitch at end, but that of *lilith* without upward inflection; loud "hoo", sometimes in crescendo series of 4-10 (up to 60), about 12-20 calls per minute; various other calls.

Habitat. Wide variety of semi-open habitats from steppes and stony semi-desert to farmland and open woodland, villages and urban areas, but extending to boreal and tropical areas; tends to avoid tall and dense stands of trees and any dense vegetation, even margins or enclaves between forests; frequently perches on post, tree or telegraph wire, or even building, particularly isolated one.

Food and Feeding. Largely small mammals and birds, reptiles, amphibians, beetles, crickets (Orthoptera), earwigs (Dermaptera) and earthworms (Lumbricidae). In Germany, insects and other invertebrates comprised 72% of diet, in Netherlands 89-2%, in France 94%, in Spain 96%, and in Italy 98%; proportion of invertebrate food increases gradually from C Europe to Mediterranean, probably result of increasing scarcity of vole (*Microtus*) prey in Mediterranean community. Perhaps deliberately takes plant material, chiefly grass and other leaves but including small fruits, berries and maize (*Zea*). Hunting essentially nocturnal and crepuscular, mainly dusk to midnight, then break of 2 hours before resumption to dawn; rarely diurnal. Hunts by perching on post or similar vantage point, dropping on prey; occasionally hovers; also hunts on ground, can run rapidly while chasing prey; larger prey taken with feet, smaller prey with bill. Beetles swallowed whole or sometimes held up in foot to be bitten 2-3 times; earthworms swallowed in single snap; prey accumulations presumed to be true caches of 30 or more items recorded.

Breeding. Season Mar-Aug. Monogamous, pair-bond often persisting all year and perhaps until partner dies. Nest in cavity, hole cleaned and hollow scraped; recorded sharing nest tree with Common Barn-owl (*Tyto alba*), also sharing hollow tree with Common Kestrel (*Falco tinnunculus*) and Common Wren (*Troglodytes troglodytes*); accepts nestboxes; some nest-sites in Britain used for over 25 years. 3-6 eggs, usually laid at 2-day intervals; lost clutches not often replaced; incubation 28-33 days, by female, reports of male incubating require confirmation; hatching either asynchronous or nearly synchronous; chick with grey-mottled down; female broods until young 14 days old, leaving nest only for brief periods, relying on male for food, both sexes leading after 14 days; young sometimes leave nest before fledging, hide in surrounding vegetation, fledge generally at 30-35 days, cared for and fed by both parents for 1 month after. In Germany, average 4.2 eggs/clutch recorded, average 2.4 young left nest hole, breeding success 58%; in Germany and Netherlands, mortality in first year of life 70%, annual adult mortality 35%; second broods rare.

Movements. Essentially resident; first-year birds disperse somewhat, but most settle within 20 km of natal site. Accidental Ireland (from introduced British population), Norway, Sweden, Finland, Estonia, Malta and Canary Is.

Status and Conservation. Not globally threatened. CITES II. Best current (mid 1990's) population estimates for Europe, expressed as number of breeding pairs: Iberia 88,000; Italy and France each 22,000; Britain 9000; Netherlands 11,000; Germany 7000; E & SE Europe 90,000; Russia up to 100,000; Turkey perhaps 20,000. In prime habitats such as in the French Massif Central and around the Black Sea, densities may reach 2-2 pairs/km². No reliable data for rest of range. Population fluctuates, especially in N of range, where marked decreases recorded after severe winters. Range has contracted locally in many parts of Europe, ascribed mainly to habitat changes, including loss of suitable nest-sites and, less often, pesticides; decreases reported in Britain, France, Belgium, Netherlands, Luxembourg, Germany, Denmark, Poland, Czech Republic, Slovakia, Austria, Switzerland, Italy and Greece. Numbers in Netherlands declined by probably over 50% during 1970-90, qualifying species for national Red List; industrialized farming practices largely responsible, reducing foodstocks such as voles and earthworms. In Britain, humans caused 35 of 52 breeding failures (67%) by various means, including taking eggs, shooting, deliberately blocking nest chambers, and disturbance by machinery. In C Europe, pastures and meadows flanked by pollard trees afford ample nest-sites and hunting lookout posts, and year-round short herbage with plenty of invertebrate prey provides optimal habitat; however, carrying capacity can be prejudiced by intensification of agricultural methods, ground clearance, reduced availability of nest holes through tree-felling and demolition or repair of old buildings, excessive use of toxic chemicals, and road-traffic deaths; such injurious factors can be partially offset by conservation, and where necessary by regular pollarding of old nesting trees and provision of nestboxes (as e.g. in Belgium and Germany) to replace lost natural holes. Species will adopt alternative nesting places, including crevices in ruins, windmills and adobe buildings.

Bibliography. Al-Mehim *et al.* (1997), Ali & Ripley (1981), Arias (1994), Ash & Miskell (1998), Aspinall (1996), Augst & Manka (1997), Bannerman (1953), Beaman & Madge (1998), Breuer (1998), Cave & Macdonald (1955), Coppee *et al.* (1995), Cramp (1985), Diaz, Asensio & Telleria (1996), Dombrowski *et al.* (1991), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Échécopar & Hue (1964, 1978), Evans (1994), Eko (1988, 1989, 1990, 1992), Eko & Hennes (1980), Eko & Scherzinger (1989), Fajardo & Babiloni (1996a, 1996b), Fajardo & Pividal (1998), Finck (1989, 1990, 1993), Flint *et al.* (1984), Friedmann (1930), Fronezak &

Dombrowski (1991), Fry *et al.* (1988), Gassman & Bäumer (1993), Gassman *et al.* (1994), Génat (1989, 1990a, 1990b, 1991, 1992), Génat & Bersuder (1995), Génat & Lecomte (1998), Glue & Scott (1980), Goodman (1988), Goodman *et al.* (1989), Gorman (1995), Gragera (1996), Grimmett *et al.* (1998), Hagemeijer & Blair (1997), Handrinos & Akriotis (1997), Hernández (1988), Higgins (1999), Hue & Échécopar (1970), Hurstel (1991), Ille (1992), Illner (1990, 1991), Jennings (1995), Juillard (1980, 1984, 1989), Juillard *et al.* (1990), Kämpfer-Lauenstein & Lederer (1988, 1995), Kemp & Kemp (1998), Kinsky (1973), Labitte (1951), Lecomte (1995), Ledant *et al.* (1981), Lei Fumin (1995), Lei Fumin & Cheng Tsohsin (1995), Lei Fumin & Yin Zuohua (1998), Lever (1987), Loske (1986), Lucas (1996), Mackworth-Præd & Grant (1957, 1970), Máñez (1981, 1983, 1994b), Marchant *et al.* (1990), Martin, B.P. (1992), Martínez, J.A., Izquierdo *et al.* (1996), Meisser (1995), Mendelssohn (1996), Mienis (1979), Mikkola (1983), Millán (1994), Negro *et al.* (1990), Obuch & Kürthy (1995), Paz (1987), Porter, Christensen & Schiermacker-Hansen (1996), Purroy (1997), Ripley (1982), Roberts (1991), Robiller & Robiller (1986), Rogacheva (1992), Rutgers & Norris (1972), Sane & Hurstel (1996), Scherzinger (1990), Schönn *et al.* (1991), Shirihai (1996), Simeonov *et al.* (1990), Snow (1978), Snow & Perrins (1998), Stepanyan (1990), Stocks (1996), Voous (1988), Zhao Zhengjie (1995), van Zoest & Fuchs (1988).

153. Spotted Owlet

Athene brama

French: Chevêche brame

German: Brahmakauz

Spanish: Mochuelo Brahmán

Other common names: Spotted Little Owl

Taxonomy. *Strix brama* Temminck, 1821, Pondicherry.

Probably forms superspecies with *A. noctua*. Birds from NE Assam sometimes separated subspecifically as *ultra*. Putative Tibetan form "*poikila*" apparently referable to *Aegolius funereus*. Four subspecies recognized.

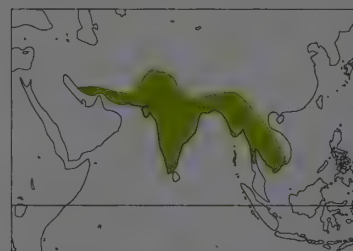
Subspecies and Distribution.

A. b. albida Koelz, 1950 - S Iran and S Pakistan; possibly also S Afghanistan.

A. b. indica (Franklin, 1831) - N & C Indian Subcontinent.

A. b. brama (Temminck, 1821) - S India.

A. b. pulchra Hume, 1873 - Myanmar, Thailand (except S half of peninsula), S Laos, Cambodia and S Vietnam.



Descriptive notes. 19-21 cm; c. 115 g. Rounded head, with heavily spotted crown, darkish facial disc bordered white around sides; curved white eyebrows; above, grey-brown with scattered white spots; flight-feathers and wing-coverts mottled or spotted white; short tail narrowly and rather indistinctly banded, lacking conspicuous white tip; breast creamy-white with short dark grey to brownish bars; broad white gorget; tarsi long and thin, with short feathers to base of toes; iris golden-yellow; bill greenish-horn, yellow on culmen; feet yellowish-green. Differs from *A. noctua* in boldly barred underparts and slightly

smaller size. Races distinguished by colour intensity and size: *pulchra* small, dark, with heavier spotting; *indica* paler and browner; *albida* palest. Voice. Medley of harsh screeches, chatters and chuckles; breeding call "chiurr chiurr chiurr..." interspersed with "cheevah cheevah cheevah..."; sometimes discordant duets; territorial call plaintive double whistle, "plew plew"; non-breeding call "chevak-vak-cheevak-vak-vak-vak...", separately or interspersed with "chev-vuv-vuv-chev-vuv-vuv...", and "sev-sev-sev..."; aggressive call sounds like normal call but higher-pitched; alarm loud screeches.

Habitat. Towns, agricultural fields, open forest, desert and semi-desert, and mango groves, from lowlands to 1500 m; avoids dense forest.

Food and Feeding. Mainly small insects; also small roosting birds, mice, shrews (Soricidae) and geckos (Gekkonidae). Rodents comprise 61% of biomass but only 15% of prey items. Leaves roost c. 15 minutes after sunset. Hunts mainly from perch; occasionally hovers before swooping on prey; several individuals sometimes congregate at night while hunting insects near electric lights.

Breeding. Lays Dec-Apr; peak months vary annually, probably dependent on food availability or photoperiod. Nest in tree cavity, chimney, under ceiling or roof, in loft or eaves; appropriates cavities from mynas (Sturnidae), especially *Acridotheres*, parakeets (*Psittacula*) and rollers (*Coracias*); reported sometimes to line nest with feathers of other species; copulation occurs in twilight. Incubation behaviour begins before eggs laid. Usually 2-3 eggs (up to 5); female incubates, sits tight when nest approached, male also said to incubate but confirmation required; incubation period 28-32 days; eggs hatch synchronously; both male and female feed nestlings; no evidence of nest sanitation, faecal sacs and broken eggs left in nest; fledging period c. 32 days, young remain with adults for 3 weeks after fledging, often seen in family groups of 3-4. Nest success 50-65%.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Tolerates human activity and habitation, calling from roofs of houses and hunting around street lights. Common over most of range, though rare in S Vietnam.

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154. Forest Owlet

Athene blewitti

French: Chevêche forestière

German: Blewitkauz

Spanish: Mochuelo de Blewitt

Other common names: Indian Forest Owlet, Forest Spotted Owlet/Owl, Forest Little Owl, Blewitt's Owl

Taxonomy. *Heteroglaux Blewitti* Hume, 1873, Busnah, Phooljan State, India.

Relationships uncertain; possibly more closely related to *Glaucidium*. Monotypic.

Distribution. WC & EC India: plains and low foothills of Akran Range (W end of Satpura Mts) near Tapi (Tapti) R in NW Maharashtra (formerly W Khandesh), and probably in E Madhya Pradesh and W Orissa (no records in 20th century from last two).



Descriptive notes. 20-23 cm. Facial disc mostly white with fine light brown barring; crown grey-brown with faint, sparse pale spots (appears unspotted); mantle and back unspotted dark grey-brown, with obsolete hind-collar; brown scapulars marked with large white spots; flight-feathers and tail with broad bars of dark brown and white, tail broadly tipped white except in worn plumage; below, mostly white, with dark brown bar across throat; breast almost uniform grey-brown, upper flanks broadly barred dark brown, lower breast, belly, lower flanks, heavy tarsal feathering and undertail-coverts white; iris yellow; bill yellowish or

greenish-horn. Flight direct, not undulating. Differs from other *Athene* in relatively short broad wings, very heavy tarsi, large claws; distinguished from adult *A. brama* by lack of spotting on head, and from all ages of latter by plumage more uniform above and more contrasting below and on wings and tail, different face pattern and heavily white-feathered toes. Juvenile undescribed. Voice. Primary song a series of quick, sweet, plaintive well-spaced notes of 1-2 syllables, given by day; also hissing and screeching calls.

Habitat. Dry to dense moist lowland deciduous forest at 200-500 m; once found in a streamside mango grove. Often perches in shady middle stratum of forest in hot weather.

Food and Feeding. Little information; 1 of 2 individuals seen in Nov 1997 had blood on bill, indicating that vertebrates (mammals or birds?) probably form part of diet, although not much harassed by small birds, which show little fear of it; also observed eating a fair-sized lizard by day, and foraging on rain-soaked ground, presumably for insects. Strongly diurnal; perches in bare tree-tops in full sun, flicking tail.

Breeding. No information.

Movements. Apparently resident; birds were still present at the Nov 1997 rediscovery site in Jun 1998 and subsequently.

Status and Conservation. CRITICALLY ENDANGERED. CITES I. Only 7 skin specimens, indicating historical rarity; last collected in 1884 from Taloda (Khandesh); claim of specimen collected in 1914 recently shown to be fraudulent. Presumed extinct until claim of 1 photographed in 1968 near Nagpur, Madhya Pradesh, but this subsequently rejected as misidentified *A. brama*; several other photographs and sight records since 1950's from S Rajasthan and S Bihar either misidentified or unsatisfactory. Unsuccessful searches in 1975-76 in 3 areas along Tapi (Tapti) R and 2 in Orissa, and in 1997 in 4 areas in E of range. No indisputable records until 2 birds (possibly pair) seen, photographed and videotaped in Nov 1997 near Shahada, N of Tapi R. Clearly threatened by habitat destruction, as it is thus known only from lowland forest in areas with increasing human pressure.

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155. Burrowing Owl

Athene cunicularia

French: Chevêche des terriers **German:** Kaninchenkauz **Spanish:** Mochuelo de Madriguera

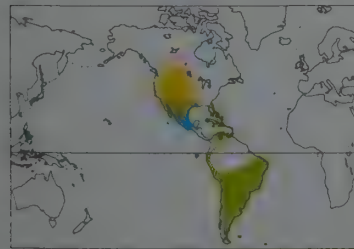
Taxonomy. *Strix Cunicularia* Molina, 1782, Chile.

Sometimes placed in separate monotypic genus *Speotyto* on basis of morphological and karyotypic differences, but osteological features and DNA support inclusion in *Athene*. Some of the races described could reflect merely individual variation or intergrading populations, and thus probably not acceptable; subspecific taxa and delimitations require critical re-evaluation with modern systematic methods, although some certainly appear distinct. Lesser Antilles races *amaura* and *guadeloupensis* extinct. Nineteen extant subspecies recognized.

Subspecies and Distribution.

- A. c. hypugaea* (Bonaparte, 1825) - from S Canada, W of E edge of Great Plains, S to El Salvador.
- A. c. rostrata* (C. H. Townsend, 1890) - Clarion I in Revillagigedo Is (off W Mexico).
- A. c. floridana* (Ridgway, 1874) - Florida (also, marginally, Georgia) and Bahamas; also (possibly this race) Cuba and I of Pines.
- A. c. troglodytes* (Wetmore & Swales, 1931) - Hispaniola, including Gonâve I and Beata I.
- A. c. arubensis* (Cory, 1915) - Aruba (Netherlands Antilles).
- A. c. brachyptera* (Richmond, 1896) - Margarita I, off N Venezuela.
- A. c. apurensis* (Gilliard, 1940) - NC Venezuela.
- A. c. minor* (Cory, 1918) - S Guyana and extreme N Brazil (Roraima).
- A. c. carrikeri* (Stone, 1922) - E Colombia.
- A. c. tolimae* (Stone, 1899) - W Colombia.
- A. c. pichinchae* (von Boetticher, 1929) - W Ecuador.
- A. c. punensis* (Chapman, 1914) - SW Ecuador, NW Peru.
- A. c. intermedia* (Cory, 1915) - W Peru.
- A. c. nanensis* (Berlepsch & Stolzmann, 1892) - SW Peru.
- A. c. juninensis* (Berlepsch & Stolzmann, 1902) - C Peru to W Bolivia and NW Argentina.
- A. c. boliviana* (L. Kelso, 1939) - Bolivia.
- A. c. grallaria* (Temminck, 1822) - C & E Brazil.
- A. c. partridgei* Olog, 1976 - NE Argentina (Corrientes).
- A. c. cunicularia* (Molina, 1782) - S Bolivia and S Brazil S to Tierra del Fuego.

Descriptive notes. 19-25 cm; male 130-185 g, female 120-250 g. Head round; distinct oval facial ruff, broad buff-white eyebrow to malar stripe; upperparts brown, with crown, back and scapulars spotted pale brown-buff to buff-white; wings long and rounded, with 10 brown and buff-white barred primaries; tail short, with 12 similarly barred rectrices; underparts buff-white with broad brown barring, throat and undertail-coverts white; eyes lemon-yellow, bill cream; legs long, with white to beige feathers, toes bristled. Sexes similar; female more heavily barred below, male slightly lighter and dorsally more grey-brown during summer. Juvenile brown above, streaked or spotted buff-white, with band of unspotted brown feathers between



nape and back; dark brown ground colour on anterior wing and tail contrasts with lighter median secondary coverts, producing light band on upperwing; chest dark brown. Races vary mainly in biometrics, in depth of coloration and in strength and extent of markings; suggested that W North American races larger than Caribbean and tropical ones, but datasets for *floridana* and *hypugaea* show little difference; *grallaria* with much buff in plumage. Voice. "Coo coooo" given exclusively by male; male also gives series of 5-8 high-pitched and raspy "chéh" notes, first longer, followed by longer pause, and the rest close together, rather rhythmically, lasting c. 1-2 seconds in total; female copulatory call is series of downslurred notes or warble.

Habitat. Dry and open habitats: treeless plains, grassland, prairie, savanna, desert or farmland; golf courses, cemeteries, road verges (even within cities), airports, vacant lots in residential areas, campuses and showgrounds; from sea-level to 4500 m. Often associated with burrowing animals: for most populations, burrow a critical habitat requirement, though some excavate own burrow (e.g. in Florida). **Food and Feeding.** Primarily arthropods and small mammals; also amphibians and reptiles. In Oregon, invertebrates made up 91.6% of diet by number but only 22% by weight; small vertebrates, mostly mammals, comprised 8.4% of individuals and 78% of biomass. In Arizona, scorpions (Scorpionida), beetles (Coleoptera), cicadas (Cicadidae) and small rodents (Heteromyidae) most frequent in summer pellets. In California, beetles, crickets (Orthoptera) and meadow voles (*Microtus*) most frequent, and earwigs (Dermaptera) common both winter and early summer; however, pellets can be poor indicators of food habits, given differences in way prey consumed or rate at which remains decomposed. In Florida, amphibians and reptiles especially important. Crepuscular, though hunting over 24 hours observed; insects taken during daylight, small mammals after dark. Hunts by walking, hopping or running along ground; also flies from perch, hovers over tall vegetation, and flycatches in air; hunting style connected to type and activity of prey, time of day and vegetative substrate. Prey caught with feet; may be transferred to bill for carrying or presentation to young; food items also sometimes found in nest burrow or tunnel during breeding season, or in food caches scattered through hunting area.

Breeding. Season Mar-Aug. Monogamous, occasionally polygynous; both pair-retention and pair-splitting observed; duration of pair-bond varies among races. Nest in burrow, either isolated or near other burrows, sometimes close to road, can be surrounded by bare ground or in grazed and level pasture, sometimes high perches nearby; in Florida often excavates own burrow, and sites concentrated in residential and industrial areas where development occupies 25-75% of landscape, with burrows typically in elevated areas, presumably to protect from flooding; in Caribbean too, will excavate hole where burrowing animals absent; in general, however, uses burrow dug by mammal such as ground squirrel (*Spermophilus*), American badger (*Taxidea*), prairie dog (*Cynomys*), marmot (*Marmota*), skunk (*Mephitis*, *Spilogale*), armadillo (*Dasypus*), kangaroo rat (*Dipodomys*), or by gopher tortoise (*Gopherus*); burrow renovated and maintained by digging and kicking backwards with feet, and digging with bill. Courtship displays include circular flights by male, mutual billing and preening of head and facial areas, presentation of food by male to female, and male song. Clutch c. 6-11 eggs; incubation 28-30 days; female does all incubating and brooding, male does all hunting, female begins to hunt as young become less dependent; chick partly covered with down (tilopaedic), altricial; fledging period c. 44 days; young stay in area of nest burrow and join parents on foraging flights at dusk. Fledging success in old burrows 63%, in newly excavated ones 19%; reproductive success varies from 100% of attempts (New Mexico) to 33% (California), 1.6-4.9 fledged per nest attempt; no information on lifetime reproductive success, though in California reproductive extinction observed in a population in half time predicted by population models. Age at first breeding 1 year. Longest known lifespan observed in ringed wild individual 8.6 years.

Movements. Most N populations migrate or disperse; little information on routes, times and wintering areas; those breeding in S Canada and N USA probably migrate S, those in SW & SC USA (New Mexico, Colorado, Texas, Oklahoma) migrate or disperse widely. Remaining populations breeding S from California and Florida essentially non-migratory.

Status and Conservation. Not globally threatened. CITES II. Listed as endangered in Minnesota and Iowa, and species of special concern in Washington, Oregon, California, Montana, Idaho, Wyoming, Utah, North and South Dakota, Oklahoma and Florida; designated as endangered in British Columbia and Manitoba, and threatened in Alberta and Saskatchewan. Still relatively numerous in parts of North American range (e.g. of 24 jurisdictions in W USA, 46% reported a population size between 1000 and 10,000 pairs in early 1990's), but declining seriously in many areas. Considered common to fairly common in Mexico; locally common in Cuba and Hispaniola, and fairly common in most of the Bahamas, but declining in Grand Bahama and New Providence; widespread and locally common in South America, though reported as virtually extinct in Tierra del Fuego. Race *amaura* of Nevis, St Kitts and Antigua and *guadeloupensis* of Guadeloupe and nearby Marie Galante extirpated c. 1890. In Florida, however, where population estimated 3000-10,000 adults in late 1980's, range expansion N to Georgia since 1950's; human activities actually beneficial where mowing, cattle grazing and wetland drainage have increased range, residential and industrial areas supporting largest concentrations. Activities causing decline include intensive cultivation of grassland and native prairies, resulting in 21% loss of habitat over 7 years in Saskatchewan; intensive agriculture, resulting in loss of burrows and foraging areas, degradation of nesting habitat, greater vulnerability to predation, and potential impeding of pair formation; collisions with vehicles; disturbance at nest- and roost-sites from dogs, people and construction work; shooting and trapping; and pesticides and other contaminants and toxins, resulting in either direct toxicity or indirect mortality from contaminated prey, though latter effect needs further study. Proposed management strategies include protecting burrowing-mammal populations, placing wood or plastic nestboxes in ground, providing artificial perches for hunting and predator observation, and managing vegetation through fire or grazing. In Canada, use of carbofuran insecticide already prohibited within 250 m of occupied nest burrows, though prohibition appears to be ineffective despite promotion; some Canadian provinces protect private land from cultivation and reseeded through monetary and voluntary lease agreements. In Florida, signs placed near burrows to educate public, but action did not significantly affect fledging and territory-reoccupancy rates. Reintroductions attempted in British Columbia, Manitoba and Minnesota; in British Columbia, 91 fledglings produced as of 1986, but no returns of reintroduced young recorded in either Manitoba or Minnesota.

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(1966), Stiles & Skutch (1989), Stocks (1996), Stotz *et al.* (1996), Sykes (1974), Thompson & Anderson (1988), Thurber *et al.* (1987), Trulio (1995), Turk (1997a), Tyler, H.A. & Phillips (1978), Tyler, J.D. (1983), Urban (1959), Vocus (1983, 1988), Walker (1993), Wedgwood (1976, 1979), Wetmore (1926, 1968a), Wetmore & Swales (1931), Wiley (1986b), Wolfe & de la Torre (1990), Zimmer (1930).

Tribe AEGOLIINI

Genus AEGOLIUS Kaup, 1829

156. Boreal Owl

Aegolius funereus

French: Nyctale de Tengmalm **German:** Rauhfußkauz **Spanish:** Mochuelo Boreal
Other common names: Tengmalm's Owl

Taxonomy. *Strix funerea* Linnaeus, 1758, Sweden.

Races *pallens* and *magnus* intergrade in Yakutsk area; these populations sometimes separated as race *jakutorum*. Nominative and *pallens* intergrade in W Asia. Proposed race *sibiricus* included within *pallens*. "*Athene brama poikila*" apparently referable to present species. Six subspecies recognized.

Subspecies and Distribution.

A. f. funereus (Linnaeus, 1758) - Europe from N Scandinavia S to Pyrenees and then E to Urals, excluding Caucasus.

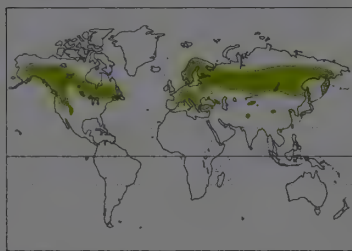
A. f. caucasicus (Buturlin, 1907) - Caucasus; possibly this race or nominate in N Turkey.

A. f. pallens (Schalow, 1908) - W Siberia, Tien Shan, and S Siberia E through NE China (Heilongjiang) to Russian Far East (including Sakhalin).

A. f. magnus (Buturlin, 1907) - NE Siberia, from Kolyma to Kamchatka.

A. f. heickianus Stresemann, 1928 - NW India (Lahul) and W China (Qinghai).

A. f. richardsoni (Bonaparte, 1838) - North America (from C Alaska S to W USA, and E through Canada to Labrador).



Descriptive notes. Male 21–25 cm, 90–115 g; female 25–28 cm, 120–195 g. Conspicuous grey-white facial disc, framed by brown-black border and highlighted by white raised eyebrows; crown umber-brown with numerous small white spots; upperparts brown, with large white spots on scapulars and small white spots on back and rump; primaries with no more than 5 rows of white spots; tail with 3 rows of spots remaining isolated even when tail closely folded; underparts creamy-white, broadly streaked brown to russet; eyes yellow; bill waxy yellow to horn; legs and toes thickly feathered to claws. Distinguished from *A.*

acadicus by larger size, yellow bill, stronger border to facial disc. Juvenile with upperparts completely dull chocolate-brown, underparts brown, facial disc dark brown with black fringe along border. Races differ mainly in coloration: in Eurasia, *magnus* largest and brightest; Nearctic *richardsoni* darkest race. **VOICE.** Male's primary advertisement a "staccato song", series of trills that increase in volume, resembling winnowing of Common Snipe (*Gallinago gallinago*); singing bouts frequently last 20 minutes but may extend to 2–3 hours.

Habitat. Boreal and subalpine forest and mixed woodland. In Europe, breeds in montane pine (*Pinus*), pine-spruce (*Picea*) and birch (*Betula*) forest, old forest stands with beech (*Fagus*), and coniferous forest with mature trees; in North America, occurs in forest characterized by black and white spruce (*Picea mariana*, *P. glauca*), aspen and poplar (*Populus*), birch and balsam fir (*Abies balsamea*), old aspen and mixed-forest sites, and subalpine forest characterized by subalpine fir (*A. lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). In winter favours mature forest, where uncrusted snow facilitates access to prey; likewise, in summer, mature forest sites have less herbaceous cover than open sites, allowing greater access to prey. Following spring thaw, shifts to openings where vole densities exceed those in forested stands; sometimes hunts over clear-felled areas and agricultural fields.

Food and Feeding. Small mammals, birds and insects; diet includes shrews (*Sorex*), red-backed voles (*Clethrionomys rutilus*) and other voles (*Microtus*), Common Chaffinch (*Fringilla coelebs*), Nearctic thrushes (*Catharus*) and beetles. Nocturnal, except in N regions without summer darkness. A sit-and-wait predator, not a pursuer; moves through forest in zigzag pattern, flying short distances between perches; after detecting prey, waits 10 minutes or more before attacking (if prey not in vulnerable position); usually attacks prey within 10 m of perch. Can capture prey under snow or vegetation; ability to locate aurally attributed to extreme asymmetry of skull, which permits localization of sounds in vertical as well as horizontal direction. Smaller prey consumed whole (head first) or piecemeal; larger ones also eaten piecemeal, with head consumed first, beginning with rear of cranium and brain; sometimes discards stomach and intestines of red-backed voles before consumption.

Breeding. Season Mar-Jul. Monogamous, polygynous and polyandrous; cases of polygyny and polyandry coincide with peaks in vole numbers; pair-bond usually lasts 1 season. In North America, nest primarily in hole of Pileated Woodpecker (*Dryocopus pileatus*) or Northern Flicker (*Colaptes auratus*); in Europe, uses Black Woodpecker (*D. martius*) cavities and nestboxes; also natural site in stand of mature or older forest, but owing to removal of large trees and snags many populations now rely almost entirely on nestboxes (more than 90% in Fennoscandia). Male sings from 1–5 potential nest cavities; after attracting female to area, demonstrates from each cavity and apparently female chooses one. 3–6 eggs, occasionally up to 11, average clutch size from 3–25 (Idaho) to 5–6 (Finland); multiple clutches common in good vole years; incubation period 29 days; female incubates and broods; male feeds female during incubation, but rarely remains near nest while roosting or foraging, brings all food to nest for first 3 weeks, then female may help supply food; chicks hatch with short white down, eyes closed, cannot lift head or stand on feet; fledging period 28–36 days; fledglings remain within 100 m of nest in loose group for 1 week or more, utter begging calls after dark and fed by parents, with time move farther from nest, but fed by adults for at least 2 more weeks, reach independence 3–6 weeks after leaving nest cavity. In 2 good vole years,

bigamous males reared average 7.8 and 9.5 fledglings/male compared with 4.2 and 5.1 for monogamous males, but no difference in number of eggs or nestling mortality for biandrous versus monoandrous females; in Idaho, 10 of 16 nests produced no young, and successful nests produced average of 2.3 fledglings; in Finland, lifetime reproduction of 141 males averaged 5.2 fledglings, first-year male annual survival was 50% and adult male annual survival 72%. Sexual maturity and breeding within 1 year of hatching. Breeding males remain in breeding population 1.5 years, have lifespan of 3–5 years.

Movements. Generally year-round resident within stable home range, but disperses in years when prey scarce. May partially migrate: adult males resident, females and young migratory. In Finland, adult females disperse up to 580 km between successive breeding seasons, while males rarely move more than 5 km; during prey declines, more than half of all females in Sweden nomadic. Accidental in Britain; NE Siberian race *magnus* accidental in Alaska.

Status and Conservation. Not globally threatened. CITES II. Population estimates largely conjectural, even in Europe, owing to species' elusive nature and mostly nocturnal habits, and primary association with relatively inaccessible areas of coniferous forest. European strongholds in Sweden (10,000–40,000 pairs) and Finland (8000–20,000 pairs), with somewhat fewer in Norway, Baltic States and Belarus, and lesser numbers in scattering of countries from Spanish Pyrenees (discovered in late 1880's) to Poland and SE as far as Turkey (5–50 pairs) and Caucasus; no major declines reported. Russian population estimated at 10,000–100,000 pairs. Fluctuations in breeding populations increase to N and E, perhaps dependent not only on vole cycles (more important and more marked in N and E regions) but also on depth of annual snow cover, since feeding inhibited by deep snow. Nestboxes employed extensively in Europe to monitor demographic characteristics, e.g. by ringing nestlings, as well as to mitigate loss of nest-sites; c. 11,000 boxes installed in Finland from which fledglings ringed annually. In North America, lack of information on demography, local and regional populations and responses to habitat change makes assessment of conservation status difficult; designated "sensitive species" in USA (USDA Forest Service Regions 1, 2, 3 and 4). Indirect effects of forest-cutting probably greatest human influence: timber-harvesting can reduce primary prey populations, remove forest structure necessary for foraging, and eliminate nest cavities, but selective harvesting may allow tree removal while maintaining suitable habitat; current management in USA involves retaining large-diameter snags in clear-felled areas and establishing nestboxes to monitor populations, also retaining aspen for nesting. Long-term effectiveness of snag retention on clear-felled sites unknown. Because forest succession is slow in spruce-fir forest, management must acknowledge that clear-felled sites will remain unsuitable for roosting or foraging for up to a century, and new nest trees will not develop for up to 2 centuries.

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157. Northern Saw-whet Owl

Aegolius acadicus

French: Petite Nyctale **German:** Sägekauz **Spanish:** Mochuelo Cabezon
Other common names: Saw-whet Owl; Queen Charlotte Owl (*brooksi*)

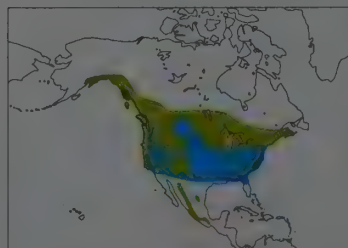
Taxonomy. *Strix acadica* J. F. Gmelin, 1788, Nova Scotia.

Possibly forms superspecies with *A. ridgwayi*, although ranges appear to overlap in S Mexico (with apparent hybridization); perhaps conspecific with latter; further study needed. Proposed race *brodkorbi* from Sierra Madre in Oaxaca based on a single juvenile specimen. Two subspecies recognized.

Subspecies and Distribution.

A. a. acadicus (J. F. Gmelin, 1788) - from S Alaska S to S USA, E to SE Canada and N Florida; also highlands of Mexico from NE Sonora to C Michoacán, E in C highlands to Puebla, Hidalgo and C Oaxaca, with isolated population in SE Coahuila, SW Nuevo León and N San Luis Potosí.

A. a. brooksi (Fleming, 1916) - Queen Charlotte Is (British Columbia).



Descriptive notes. Male 18–20 cm, c. 75 g; female 20–21.5 cm, c. 100 g. Small owl with large, rounded head. Head greyish-brown, with white streaks on crown; facial disc round, white above and between eyes; upperparts warm brown, with white spots on nape, scapulars and wing-coverts; wings rounded, outer webs of outer primaries spotted with white along edge; tail short, with 2 or 3 interrupted narrow bands of white, and margined at tip with white; underparts white, tinged or suffused buff and broadly striped or spotted rufous-brown; eyes yellow to golden; bill black; legs short, heavily feathered to talons,

pale buff to cinnamon-buff. Differs from *A. funereus* in smaller size, no black edge to facial disc, black bill, streaked (not spotted) crown; from *Glaucidium californicum* in larger size, bigger head, relatively shorter tail, more conspicuous facial disc. Juvenile lacks white markings above, except on wings and tail, and has unmarked brown breast and buff belly, and black-brown facial disc with conspicuous Y-shaped white marking between and above eyes. Race *brooksi* darker and much less

spotted above, rich orange-buff below. VOICE. Male advertising call a monotonous series of whistled notes on constant pitch, about 2 per second; female version softer, less constant in pitch and amplitude; also short series of "ksew-ksew-ksew", like sound produced by filing (whetting) large mill saw.

Habitat. Woodland, with highest densities in coniferous forest at moderate elevations and latitudes. Occurs in red spruce (*Picea rubens*) forest in North Carolina, northern white cedar (*Thuja occidentalis*) and tamarack (*Larix laricina*) swamps and red pine (*Pinus*) forest in NE USA and SE Canada, and riparian areas characterized by large white spruce (*Picea glauca*), balsam poplar and aspen (*Populus*) copses in C Canada; also in deciduous riparian woodland amid shrub-steppe desert in SW Idaho. Relatively dense populations in lower- to middle-elevation forest of ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), western red cedar (*Thuja plicata*), grand fir (*Abies grandis*) and western larch (*Larix occidentalis*); lower numbers in subalpine forest of Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta* var. *latifolia*) and subalpine fir (*Abies lasiocarpa*), usually restricted to riparian situations. In winter, wide range of habitats, varying in altitude, latitude and vegetation type; various rural and even suburban environments. Presence of dense vegetation for roosting and perches for foraging seems critical. In Mexico, occurs at 1350-2500 m.

Food and Feeding. Small mammals, primarily deer mice (*Peromyscus*); also red-backed voles (*Clethrionomys rutilus*) and *Microtus* voles fairly common. Small birds eaten in low numbers, mostly during passerine migration when they are active at night; beetles (Coleoptera) and grasshoppers (Orthoptera) also taken; race *brooksi* along coast consumes considerable quantities of intertidal invertebrates, including amphipods, isopods, spiders and insects. Nocturnal, with occasional diurnal foraging. Hunts from perch on low branch, shrub or fence post, usually in forest opening and other habitat edges. Prey detected by excellent hearing and low-light vision; caught with feet and swallowed in pieces, starting with head; larger prey consumed as 2 meals; avian prey plucked before consumption.

Breeding. Season Mar-Jul. Monogamous; polygyny occurs where prey abundant; no evidence of pair-bond lasting more than 1 season. Uses nest cavity of woodpecker or nestbox; lays directly on wood chips or other debris in cavity, such as nest of squirrel (Sciuridae). Mated pairs engage in allopreening; male occasionally sings from suitable nest cavity. 5-7 eggs; second broods probably cases of sequential polyandry; female incubates and broods young; male feeds her throughout laying, incubation and brooding; incubation period 27-29 days; hatching asynchronous; chick emerges with eyes closed and with covering of white down; when youngest nestling about 18 days old, female leaves nest to roost elsewhere; male feeds young throughout, even after female leaves; after fledging, brood-members remain together outside nest, continue to be fed by male for at least 1 month. Hatching success 75% from 7 nests (30 eggs hatched from 40 laid); in British Columbia, 22 nests fledged 2-68 young/nest. Age of first breeding probably 1 year, though no data from wild populations; ringing returns indicate survival c. 40-50% per year. Longest recorded lifespan 7 years.

Movements. Present year-round in breeding range, but considerable numbers move S in autumn, at least in E North America; S movement begins Sept-Nov in E Canada and NE USA, and Oct-Nov farther S; females migrate earlier than males. Common routes are from C Ontario down Ohio R valley to Kentucky; from Atlantic coastal lowlands from Nova Scotia to North Carolina; and around L Superior from Minnesota to Wisconsin, then S and/or E; however, does not strictly adhere to these routes. In W, movements poorly documented, but probably altitudinal as well as latitudinal. Migrates throughout night, with peak movements on clear nights with W to NW winds after passage of cold front; migration suppressed by full moon and strong, gusty winds. Accidental Bermuda.

Status and Conservation. Not globally threatened. CITES II. World population conservatively estimated at 100,000-300,000 individuals. No data on trends, but probably declining slowly as habitat lost. Acceleration of logging rates in S Canada and N USA has undoubtedly reduced amount of suitable breeding habitat, particularly through loss of nesting snags; also, young regenerating forest often too thick, lacks edge habitat and open understorey favoured for foraging. In general, mature and old-growth stands seem favoured for breeding: 10 of 13 breeding-season roost-sites were in old-growth ponderosa pine and grand fir forest, despite more extensive searches in managed stands; winter habitat perhaps less critical. Seems to survive well in rural and semi-rural areas, which are extensive compared with breeding habitat, though further study needed. In terms of management, destruction of habitat, particularly nesting snags, represents greatest threat; nestboxes could mitigate loss of snags in areas that have been selectively logged or even clear-felled in small blocks; retention of woodlots in rural and residential areas would help migrating and wintering birds.

Bibliography. Armstrong (1983), Baicich & Harrison (1997), Bielefeldt & Rosenfield (1993), Binford (1989), Bosakowski & Smith (1977), Boula (1982), Bridges (1992a), Brinker & Dodge (1993), Buckholtz *et al.* (1984), Campbell *et al.* (1990), Cannings (1987, 1993), Carpenter (1989a), Carpenter & Carpenter (1993), Catling (1972), Clark, K.A. & Anderson (1997), Clark, N. (1983), Collins (1993), Cyr (1995e), Dancy (1992), Dinsmore & Clark (1991), Eckert, A.W. (1974), Eckert, K.R. (1997), Erickson *et al.* (1994), Evans & Rosenfield (1987), Follen (1981), Forbes & Warner (1974), Frost *et al.* (1989), Grove (1985), Hayward (1983), Hayward & Garton (1988), Heintzelman (1992), Hobson & Sealy (1991), Holroyd & Woods (1975), Holt & Hillis (1987), Holt & Leroux (1996), Holt *et al.* (1991), Howell & Webb (1995a), Johns *et al.* (1978), Johnsgard (1979, 1988), Kaufman (1996), Loos & Kerlinger (1993), Marks & Doremus (1988), Marks *et al.* (1989), Marti (1986), Mayfield & Alsop (1992), Miller (1990), Milling *et al.* (1994), Mueller (1982a, 1982b, 1990), Newman (1987), Norton & Holt (1982), Otter (1996), Palmer (1983, 1986, 1987), Parker (1991), Parmalee & Klippel (1987), Rains (1994), Root (1988), Rosenfield (1979), Russell *et al.* (1991), Sealy & Hobson (1987), Slack (1992a, 1992b), Slack *et al.* (1987), Small (1994), Spahn (1978), Steinberg (1996), Stotz *et al.* (1996), Strauss (1990), Swengel, A.B. (1987a, 1987b), Swengel, A.B. & Swengel (1986, 1995), Swengel, S.R. & Swengel (1987, 1992a, 1992b), Tallman (1993), Tyler & Phillips (1978), Voous (1988), Walker (1993), Weir (1989, 1990), Weir *et al.* (1980), Wolfe & de la Torre (1990).

158. Unspotted Saw-whet Owl

Aegolius ridgwayi

French: Nyctale immaculé **German:** Ridgwaykauz **Spanish:** Mochuelo Moreno

Taxonomy. *Cryptoglaux ridgwayi* Alfaro, 1905. Cerro de la Candelaria, near Escazú, Costa Rica. Possibly forms superspecies with *A. acadicus*, although ranges appear to overlap in S Mexico (with apparent hybridization). Perhaps conspecific with latter; further study needed. Validity of races uncertain; suggested that both *tacananensis* and *rostratus* perhaps in fact hybrids between present species and *A. acadicus*; further research required. Three subspecies conditionally recognized.

Subspecies and Distribution.

A. r. tacananensis R. T. Moore, 1947 - S Mexico (Chiapas).
A. r. rostratus (Griscom, 1930) - Guatemala, Honduras and El Salvador (presumed this race).
A. r. ridgwayi (Alfaro, 1905) - Costa Rica and W Panama.



Descriptive notes. 18-21 cm; 80 g. Small, large-headed and variable in colour. Plumage recalls juvenile *A. acadicus*; facial disc brown, with paler central area and narrow outer rim; broad white eyebrows; upperparts uniform grey-brown, with white markings only on wings and sometimes tail; underparts brown, yellower on belly; toes feathered almost to talons. Juvenile similar, but plumage downier, often pale streaking on chest. VOICE. Whistled "hoo hoo hoo...", 4-10 notes; similar to *A. acadicus* (but distinguishable by sonograms).

Habitat. Humid pine-oak and oak forest of highlands and cloudforest; sometimes in edges and gaps with scattered tall trees; from 1600 m to 3000 m, occasionally down to 1400 m in Guatemala.

Food and Feeding. Probably mainly small mammals, such as rodents and shrews (Soricidae), also bats, and small birds; presumably insects, too; occasionally frogs. Hunts after dusk; fluttery and agile flight with rapid wingbeats.

Breeding. Little known. Lays during Mar; nest undescribed, probably old woodpecker hole; 5-6 eggs. **Movements.** Resident, but little known.

Status and Conservation. Not globally threatened. CITES II. Currently considered Near-threatened. Generally considered uncommon. Fairly common (e.g. around San Cristóbal de las Casas, Chiapas) to uncommon in Mexico; occasional in some places in Costa Rica; rare in Panama. Needs at least patchy forest; suitable habitat decreasing. No information available on ecology or behaviour, and details of distribution very sparse.

Bibliography. Anon. (1998a), Binford (1989), Howell & Webb (1995a), Land (1970), Ridgely & Gwynne (1989), Slud (1964), Stiles & Skutch (1989), Stotz *et al.* (1996), Thurber *et al.* (1987), Wetmore (1968a).

159. Buff-fronted Owl

Aegolius harrisii

French: Nyctale de Harris **German:** Blaßstirnkauz **Spanish:** Mochuelo Canela

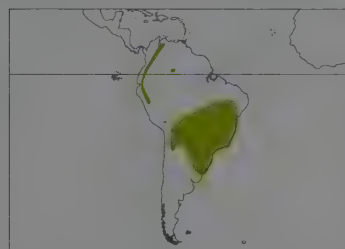
Taxonomy. *Nyctale Harrisii* Cassin, 1849, South America.

Race *iheringi* perhaps specifically distinct. Population of Cerro Neblina (S Venezuela), known only from two specimens collected in 1985, has not been subspecifically determined. Three subspecies recognized.

Subspecies and Distribution.

A. h. harrisii (Cassin, 1849) - Andes from NW Venezuela S to NC Peru.
A. h. iheringi (Sharpe, 1899) - E Bolivia, Paraguay, C & E Brazil (Ceará to Rio Grande do Sul), S to NE Argentina and NE Uruguay.
A. h. dabbenei Olog, 1979 - NW Argentina (Tucumán, Salta and Jujuy); also (possibly this race) W Bolivia.

Also (subspecies unknown) Cerro Neblina, S Venezuela.



Descriptive notes. 20-21 cm; 104-150 g. Compact, with short tail and large square head. Facial disc outlined in black with buff trim, strongly contrasting with dark head; lores to base of bill brown; forehead and collar on hindneck yellowish-buff; upperparts chocolate-brown, darkest on head; primaries notched with white, wing-coverts with white spots; tail blackish, with 2 broken white bars and white tip; small chin patch brown. Rest of underparts yellowish-buff; eyes greenish-yellow; bill pale yellow to grey; tarsi feathered cream-yellow; toes unfeathered and yellowish. Juvenile lacks buff spots above. Race *dabbenei* darker above.

tinged cinnamon below; *iheringi* dark above, scapulars variably edged buff, face and underparts deeper orange. VOICE. Whistled trill, "frunrururururu", lasting 3-4 seconds, pitched high but slightly fluctuating.

Habitat. Recorded from fairly open, humid forest to tree-line, but also in drier zones and ravines, and at forest edge: examples include *Podocarpus* and *Alnus* forest, *Araucaria* forest, *Polylepis* woodland, dry Chaco deciduous forest, *cerrado* woodland, densely timbered *caatinga*, semi-humid, rather open forest about 10 m tall, and mossy, stunted forest near tree-line; also artificial landscapes rich in fruit trees and palms. In Andes, at elevations of 1500-3800 m; elsewhere in lowlands, from sea-level to 1000 m.

Food and Feeding. Prey remains found in nest cavity included chitin of insects and bones of small rodent. Record of individual seen hovering over roadside shrub before dawn. No further information.

Breeding. Little information. In Brazil, nest with 3 eggs found in early Mar 6 m above ground in cavity of dead palm, probably abandoned hole of parrot (*Aratinga*), cavity 60 cm deep and 15 cm in diameter, with opening 10 cm across, lined with cattle dung, feathers and hairs; in Argentina, found nesting in hollow tree.

Movements. Probably resident.

Status and Conservation. Not globally threatened. CITES II. Currently considered Near-threatened. Considered generally rare throughout range, but very few data. Placed on preliminary "Blue List" in Colombia, where population believed to be declining. In Argentina, considered less scarce than generally supposed and probably overlooked: recent scattered records reported with some regularity from different parts of the country. Occurs in several protected areas, e.g. *Podocarpus* National Park, Ecuador, and Iguazú and El Rey National Parks, Argentina.

Bibliography. Barlow & Cuello (1964), Barrowclough *et al.* (1997), Blendinger (1998), Canevari *et al.* (1991), Chebez (1994), Fjeldså & Krabbe (1990), Hayes (1995), Herzog *et al.* (1997), Hilty & Brown (1986), Meyer de Schauensee & Phelps (1978), Olog (1979a, 1985), Parker *et al.* (1985), de la Peña (1994), Pereyra (1950), Rasmussen *et al.* (1996), Remsen & T aylor (1983), Saibene *et al.* (1996), Sargeant (1996), Sick (1993, 1997), Stotz *et al.* (1996), Studer & Teixeira (1994), Williams & Tobias (1994).

160

ssp rufa

ssp queenslandica

ssp humeralis

161



ssp boobook



164

ssp lurida

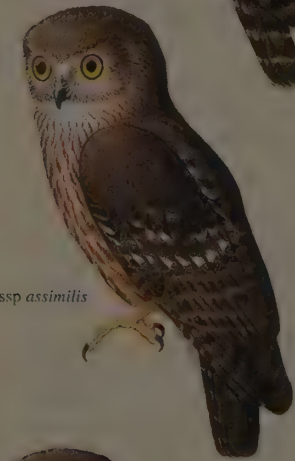


ssp fusca

164



ssp ocellata



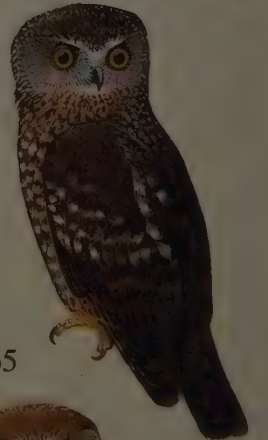
ssp assimilis

163



ssp novaeseelandiae

165



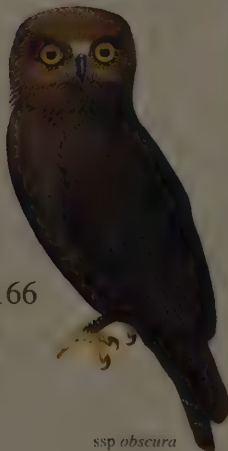
ssp leucopsis

ssp undulata



ssp scutulata

166



ssp obscura



167



168

PLATE 18

inches 7
cm 18

Tribe NINOXINI

Genus *NINOX* Hodgson, 1837

160. Rufous Owl

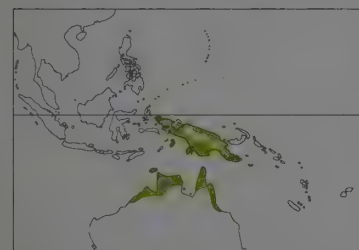
Ninox rufa

French: Ninox rousse **German:** Rostkauz **Spanish:** Ninox Rojizo
Other common names: Rufous Hawk-owl; Brown/Barred Papuan Owl (*humeralis*)

Taxonomy. *Athene rufa* Gould, 1846, Arnhem Land, Northern Territory. Sometimes considered to form superspecies with *N. strenua*. Races require revision: *meesi* possibly only a pale morph of *queenslandica*; Aru population sometimes separated as *aruensis*, but apparently indistinguishable from *humeralis*; species has even been suggested as being monotypic. Four subspecies recognized.

Subspecies and Distribution.

N. r. humeralis (Bonaparte, 1850) - New Guinea, including Aru and Waigeo Is.
N. r. rufa (Gould, 1846) - NE Western Australia (Kimberleys) and N Northern Territory (Arnhem Land).
N. r. meesi Mason & Schodde, 1980 - coastal and subcoastal Cape York, S in Queensland to about R Endeavour and R Mitchell.
N. r. queenslandica Mathews, 1911 - coastal and subcoastal Queensland from R Endeavour S to lower R Burdekin and perhaps Rockhampton.



Descriptive notes. 40-52 cm; male c. 1200 g, female c. 980 g. A large hawk-owl with rather small head and long tail. Indistinct blackish facial disc; dark rufous-brown back, with narrow light brown bars; underparts white to buff, densely barred with rufous-brown; golden-yellow eyes; grey bill. Sexes similar, female smaller. Races differ in size and intensity of colour: *humeralis* smaller and browner; *queenslandica* large and dark, with paler underparts. **VOICE.** Low, slowly repeated "woo-hoo"; female higher-pitched than male.

Habitat. Mainly upland and lowland rainforest, well-wooded savanna, monsoon woodland,

gallery forest and forest edge, especially along waterways; less common in paperbark (*Melaleuca*) forest and mangrove. Lowlands and foothills to 2000 m in New Guinea; in Australia, up to at least 1200 m. Roosts by day singly or in pairs in thick-foliaged tree or tree hollow; often roosts clutching remains of large prey.

Food and Feeding. Main prey medium-sized mammals such as marsupials (*Antechinus*, *Isodon*, *Trichosurus*, *Pseudocheirus*, *Petaurus*), rodents (*Rattus*, *Conilurus*) and fruit bats (*Pteropus*), medium and large birds such as megapodes (Megapodiidae), including Australian Brush-turkeys (*Alectura lathami*), and large insects. Nocturnal, activity beginning about dusk. Takes insects from foliage; also takes prey from ground; often moves into more open areas adjoining forest to hunt; swoops, banks and glides through canopy to snatch arboreal mammals and roosting birds.

Breeding. Not well known. Lays c. Jun-Sept, tending to be earlier in warmer areas. Monogamous and territorial. Nest in debris of large hollow in large tree, often in trunk or main limb. Intensified calling prior to breeding. Usually 2 eggs, rarely 1; incubation by female, period c. 36-38 days; chick with whitish first and second down; fledging period c. 7-8 weeks.

Movements. Resident; perhaps some local movement in wet season.

Status and Conservation. Not globally threatened. CITES II. Subspecies *queenslandica* given as rare in Australian national listing and vulnerable in Queensland state listing, c. 1000 pairs estimated; *meesi* as rare in Queensland. Uncommon to rare and sparsely distributed in New Guinea; some pressure from traditional hunting. In Australia, adversely affected by forest clearance and, perhaps, by increasing numbers of hot fires late in dry season.

Bibliography. Andrew (1992), Beehler *et al.* (1986), Bell (1970), Bishop (1987), Blakers *et al.* (1984), Bravery (1970), Coates (1985), Estberg & Braithwaite (1985), Fleay (1979), Garnett (1993), Higgins (1999), Hollands (1991), Kanowski (1998), Lindsey (1992), Macdonald (1988), Mason & Schodde (1980), McAllan & Bruce (1989), Nielsen (1995), Olsen (1998), Olsen & Marples (1993), Pizzey & Doyle (1998), Rand & Gilliard (1967), Schmid (1993), Schodde & Mason (1981, 1997), Schodde & Tidemann (1986), Simpson & Day (1998), Strahan (1994), Trounson & Trounson (1987), Young & De Lai (1997).

161. Powerful Owl

Ninox strenua

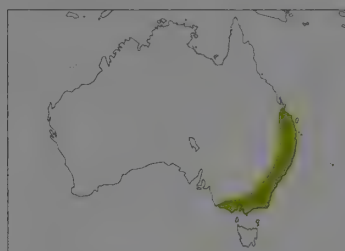
French: Ninox puissante **German:** Riesenkauz **Spanish:** Ninox Robusto
Other common names: Eagle Owl(!), Great Scrub Owl

Taxonomy. *Athene ? strenua* Gould, 1838, New South Wales.

Sometimes considered to form superspecies with *N. rufa*. Monotypic.

Distribution. Coastal and subcoastal SE Queensland (S from R Dawson), E New South Wales and SE Victoria to extreme SE South Australia.

Descriptive notes. Male 52-60 cm, c. 1500 g; female 45-58 cm, c. 1250 g. Largest hawk-owl, with proportionately small, rather rounded head and long tail. Dark grey-brown facial disc and orange-yellow eyes; dark brown to dark grey-brown upperparts with off-white barring, and flecking on crown; off-white underparts with numerous bold dark chevrons; grey bill. Differs from *N. rufa* in larger size, lack of rufous tones, coarser barring; from *N. connivens* in much bigger size, spotted crown, plainer upperparts, no streaking on underparts. Sexes similar, female smaller. Immature with upperparts more strongly barred than adult. **VOICE.** Main call is far-carrying, repeated double hoot, "woo-hoo" or "ooo-hoo"; male deeper in pitch than female.



Habitat. Open forest, especially in both wet and dry, densely forested gullies near permanent water; also woodland and scrub; occasionally in forest adjoining city parkland, pine plantations and cultivated areas, and in remnants and regeneration surrounded by logged forest; from coast up to 1500 m. Perches by day singly, in pairs or in family groups under canopy, often clutching remains of partly eaten prey.

Food and Feeding. Large arboreal vertebrates, mainly phalangers (*Pseudocheirus peregrinus*, *Trichosurus vulpecula*, *Petaurus brevipes* and *Petauroides volans*), also flying foxes (Megachiroptera) and medium-sized

roosting birds. Nocturnal, becoming active just before dusk. Swoops to snatch prey from branches and canopy; less often, takes prey from ground in more open areas; occasionally hawks flying insects.

Breeding. Lays May-Jun, earlier in N than in S. Monogamous and territorial; home range 300-1450 ha in SE. Nest in large tree hole, usually in live tree, on decayed wood; rarely in dead snag or broken-off stump. 2 eggs; incubation period c. 35-38 days; female incubates, with male main hunter; young hatch in fine white down, white second down; fledging period c. 8 weeks; some remain dependent until start of next breeding season. Mean brood size at fledging c. 1-5.

Movements. Little known. Resident and largely sedentary; permanent territory occupied throughout year; young occasionally stray inland during dispersal.

Status and Conservation. VULNERABLE. CITES II. Listed as rare or vulnerable in Australian national listing and by 3 main states in which it occurs (Queensland, New South Wales and Victoria). However, probably more common and less habitat-specific than previously supposed. Threatened by clear-felling and loss of old-growth forest to forestry operations, but can tolerate selective or light logging and survives in fragmented forest.

Bibliography. Blakers *et al.* (1984), Brouwer & Garnett (1990), Chafer (1992a), Collar *et al.* (1994), Cooke *et al.* (1997), Davey (1993), Debus (1993a, 1995, 1997a, 1997d), Debus & Chafer (1994), Evans (1986), Eyre & Schulz (1996), Fleay (1944, 1979), Garnett (1993), Gibbons (1989), Higgins (1999), Hollands (1991), Hyem (1979), James, J.W. (1980), Kavanagh (1988, 1997), Kavanagh & Bamkin (1995), Kavanagh & Peake (1993a, 1993b), Kavanagh, Debus, Tweedie & Webster (1995), Lavazanian *et al.* (1994), Lindsey (1992), Macdonald (1988), McConnell (1997), McNabb (1987, 1994a, 1994b, 1996), O'Brien (1990), Olsen, J. (1990), Olsen, P. (1998), Olsen, P. & Marples (1993), Pavey (1988, 1993, 1994, 1995), Pavey & Smyth (1998), Pavey *et al.* (1994), Pizzey (1958), Pizzey & Doyle (1998), Rose (1993), Ross (1986), Sansom (1991), Schodde & Mason (1981, 1997), Schodde & Tidemann (1986), Schulz (1997), Seebeck (1976), Simpson & Day (1998), Strahan (1994), Tilley (1982), Traill (1993), Trounson & Trounson (1987), Van Dyck & Gibbons (1980), Wallis *et al.* (1998), Wilson (1982).

162. Barking Owl

Ninox connivens

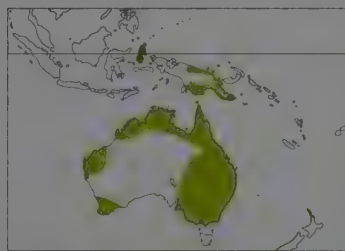
French: Ninox aboyeuse **German:** Kläfferkauz **Spanish:** Ninox Ladrador
Other common names: Barking Hawk-owl, (Northern/Western) Winking Owl

Taxonomy. *Falco connivens* Latham, 1801, Sydney region, New South Wales.

Affinities uncertain. Some authors consider species monotypic, but up to seven races accepted by others; review needed. Proposed race *occidentalis* (NW & NC Australia) has been synonymized with *peninsularis*; *addenda* (SW Australia) synonymous with nominate. Some authors have placed birds of NC Queensland in race *enigma*, but type specimen, apparently lost, reported to be either juvenile of present species or aberrant, large individual of *N. boobook*. Four subspecies currently recognized.

Subspecies and Distribution.

N. c. rufostriata (G. R. Gray, 1860) - N Moluccas (Morotai, Halmahera, Bacan, Obi).
N. c. assimilis Salvadori & D'Albertis, 1875 - C & E New Guinea W to Merauke and R Sepik, including Manam I and Karkar I.
N. c. peninsularis Salvadori, 1876 - coastal and subcoastal NW, N & NE Australia S to R Endeavour in Queensland, and islands in SW Torres Strait.
N. c. connivens (Latham, 1801) - coastal and subcoastal SW Australia, southern gulfs, and E & SE Australia (S from foot of Cape York Peninsula).



Descriptive notes. 38-44 cm; male c. 700 g, female c. 600 g (*connivens*); male c. 500 g, female c. 440 g (*peninsularis*). Medium-sized hawk-owl. Indistinct facial disc and whitish eyebrows; head and upperparts dark brown to dark greyish-brown, with bold white spots on scapulars and wing-coverts; underparts creamy-buff to whitish with bold dark brown streaks; eyes yellow; bill black. Differs from *N. boobook* in larger size, proportionately smaller head, heavier markings above; from similar-sized *N. squamipila* in streaked (not barred) underparts; from smaller *N. scutulata* in paler head, patterned upperparts. Races

assimilis and *peninsularis* smaller, with chestnut-brown streaks below; *rufostriata* browner above. **VOICE.** Mainly a distinctive, repeated, gruff, low-pitched, dog-like "wuk-wuk" by male and higher-pitched "wok-wok" by female; less often a drawn-out strangled scream; pairs often duet.

Habitat. Lowland riparian forest, forest edge, woodland and savanna up to c. 1000 m in New Guinea; dry, open sclerophyll forest and woodland in Australia; often in riparian vegetation near swamps, lakes, streams and other wetlands. Roosts by day in foliage of canopy or mid-storey, or tree hollow, often in pairs or family groups.

Food and Feeding. Large insects; also vertebrates such as possums and gliders (Phalangeridae), rabbits (*Oryctolagus cuniculus*), rodents and small to medium-sized roosting birds; occasionally reptiles. In one study, insects, although numerically dominant, never contributed more than 5% by biomass. More crepuscular than most *Ninox*, also nocturnal. Active hunter of terrestrial, arboreal or

aerial prey, mostly among trees or along forest edges. Hawks flying insects and bats in air, and makes short sallies from perch.

Breeding. Not well known. Lays mainly Jul-Sept, slightly later in S than in N. Monogamous; territorial, pairs recorded nesting 6 km apart, intensified calling prior to breeding. Nest in large open hollow in tree trunk; less often in branch, open fork of tree, or on ground. Usually 2-3 eggs (1-4); incubation c. 36 days, by female; young hatch in creamy-white down, second down whitish; fledging period c. 5-6 weeks; young disperse from natal territory by late summer. In captivity, first breed at 1 year; later in wild.

Movements. Apparently resident, but poorly known.

Status and Conservation. Not globally threatened. CITES II. Widespread throughout range. Generally thinly scattered; quite common in New Guinea, but uncommon and local in Moluccas. In SE Australia evidence of decline in population, and concern because much habitat continues to be lost and degraded by clearing and overgrazing. Listed as vulnerable in New South Wales and Victoria.

Bibliography. Andrew & Tremul (1995), Aumann (1991), Beehler *et al.* (1986), Blakers *et al.* (1984), Calaby (1951), Chaffer (1992b), Clapp (1982), Coates (1985), Coates & Bishop (1997), Davey (1993), Debus (1997b, 1997d), Debus, Shepherd & Rose (1998, 1999), Fleay (1942, 1979), Hartert (1903), Higgins (1999), Hodgson (1996), Hollands (1991), Kavanagh, Debus, Rose & Turner (1995), Kavanagh, Debus, Tweedie & Webster (1995), Kinghorn (1933), Lindsey (1992), Linsley (1995), Macdonald (1988), Mees (1964), Muir & Corke (1993), O'Brien (1990), Olsen (1998), Olsen & Marples (1993), Parker (1977a), Pizzey & Doyle (1998), Rand & Gilliard (1967), Ripley (1959), Schodde & Mason (1981, 1997), Schodde & Tidemann (1986), Schulz (1998), Simpson & Day (1998), Strahan (1994), Trounson & Trounson (1987), White & Bruce (1986), Young & De Lai (1997), Zillman (1964).

163. Sumba Boobook

Ninox rudolfi

French: Ninox de Sumba

German: Sumbakauz

Spanish: Ninox de Sumba

Other common names: Sumba Hawk-owl

Taxonomy. *Ninox rudolfi* A. B. Meyer, 1882, Sumba Island.

Sometimes considered to form superspecies with *N. boobook* and *N. novaeseelandiae*. Often treated as conspecific with *N. boobook*, which itself was formerly regarded as belonging to *N. novaeseelandiae*. Species name sometimes spelt, erroneously, *rudolfi*. Monotypic.

Distribution. Sumba I, in C Lesser Sundas.



Descriptive notes. c. 35-40 cm; female slightly larger than male. White eyebrows and chin, and yellow (or possibly brown) eyes; crown and upperparts brown, crown heavily spotted white, upperparts less so; wings and tail thinly barred; underparts whitish, strongly barred red-brown. Voice. Reported to be series of short, repeated, cough-like notes; suggests threat call of *N. boobook*, rather than usual 2-note boobook advertising call.

Habitat. Primary and tall secondary evergreen and deciduous forest, including monsoon forest, rainforest, remnant forest patches and forest edge; lowlands to c. 930 m.

Food and Feeding. Diet poorly known; probably mainly large insects. Similar in habits to *N. boobook*. Occurs singly, in pairs or loose (family?) groups of up to 4 birds.

Breeding. Apparently undescribed; 1 possible nest sighted, in cavity of huge tree.

Movements. Undescribed; probably resident.

Status and Conservation. VULNERABLE. CITES II. Restricted-range species; present in Sumba EBA. Poorly known; once more common, now uncommon or rare. Found at only 5 localities during 1989 and 1992 surveys. Threatened by extensive clearing and repeated burning for grazing and agriculture; forest now covers less than 10% of island, and there is only 1 protected area.

Bibliography. Andrew (1992), Coates & Bishop (1997), Collar *et al.* (1994), Inskipp *et al.* (1996), Jones, Juhaeni *et al.* (1994), Jones, Linsley & Marsden (1995), Mayr (1944), Mees (1964), Pitches (1998a), Stattersfield *et al.* (1998), Sujatnika & Jepson (1995), Sujatnika *et al.* (1995), White & Bruce (1986).

164. Southern Boobook

Ninox boobook

French: Ninox de Australie

German: Boobookkauz

Spanish: Ninox Australiano

Other common names: Boobook (Owl), Streaked/Northern/Australian Boobook; Red/Dark Boobook (*lurida*)

Taxonomy. *Strix Boobook* Latham, 1801, Sydney area, New South Wales.

Sometimes considered to form superspecies with *N. rudolfi* and *N. novaeseelandiae*; various other proposed treatments, e.g. as member of species-group that includes *N. novaeseelandiae*, *N. squamipila*, *N. theomacha*, *N. meeki*, *N. variegata* and perhaps other boobooks in Australasian Region; more research needed. Has often been treated as conspecific with *N. novaeseelandiae*, but separated specifically by morphological and molecular differences; Tasmanian race *leucopsis* of latter has been placed with present species, which formerly also included *N. rudolfi* as race. No consensus on number of races, much in need of revision, especially non-Australian forms. Kangaroo I population has been described as separate race (*halmaturina*), but seems not constantly separable from nearby mainland population of nominate; also, *marmorata* of SW & SC Australia synonymous with *ocellata*. Ten subspecies tentatively recognized.

Subspecies and Distribution.

N. b. rotiensis Johnstone & Darnell, 1997 - Roti.

N. b. fusca (Vieillot, 1817) - Timor.

N. b. plesseni Stresemann, 1929 - Alor.

N. b. moue Mayr, 1943 - Romang, Leti and Moa.

N. b. cinnamomina Hartert, 1906 - Babar.

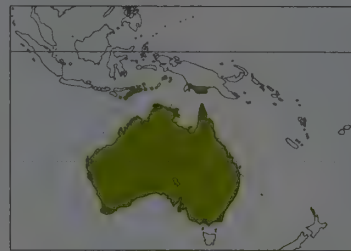
N. b. remigialis Stresemann, 1930 - Kai Is.

N. b. pusilla Mayr & Rand, 1935 - S New Guinea.

N. b. ocellata (Bonaparte, 1850) - Australia W of Great Dividing Range; rarely, islands in Torres Strait; also Sawu (W of Timor).

N. b. lurida De Vis, 1887 - NE Queensland between Cooktown and Paluma.

N. b. boobook (Latham, 1801) - coastal and subcoastal E Australia, S from S Queensland.



Descriptive notes. 25-36 cm (*pusilla* 25-28 cm, *boobook* 30-36 cm); male c. 250 g, female c. 315 g; clinal variation, smaller in warmer areas. Small, stocky and rather large-headed. Indistinct, darkish, dusky facial disc, white eyebrows; upperparts dark grey-brown or chocolate-brown with white spots; whitish below, variably spotted and streaked reddish-brown; eyes variable, yellow to hazel; feet grey or yellow. Differs from *N. novaeseelandiae* in being generally larger and paler, with less rounded wings; from *N. theomacha* in larger size and more patterned plumage. Sexes similar; female tends to have slightly more streaking/spotting on head and back than male. Juvenile tends to be more heavily streaked than adult on crown, nape and breast. Races differ in size and in intensity and extent of plumage colours and markings: all smaller than nominate; *lurida* darker chestnut-brown and lightly marked; *ocellata* paler, sandy-brown, with buff-streaked underparts; *fusca* grey-brown, heavily spotted below. Voice. Commonest call a repeated double hoot, "boo-book" or "bru-bruk".

Habitat. Wide variety, from forest, woodland, farmland, suburbs, to sparsely treed semi-deserts. In wet tropics, primary and tall secondary hill monsoon forest and woodland; generally in lowlands and foothills, but up to 2300 m on Timor. Race *lurida* found only in montane rainforest. Roosts by day in thick foliage, rarely on ground among grass or in caves or tree holes, singly, in pairs or in family groups.

Food and Feeding. Mainly insects; also, particularly when breeding, small to medium-sized vertebrates including bats, rodents, birds, lizards and frogs. Mainly nocturnal, also partly crepuscular. Hunts in forest, forest edge or out into open areas, hawking aerial insects, snatching prey from canopy and mid-storey, and pouncing on prey on ground; often hunts by moving from perch to perch; catches surplus prey in notches or crevices.

Breeding. Lays late Aug-Nov, slightly later in S than in N. Monogamous; territorial, intensified calling prior to breeding. Nest in tree hole in trunk, spout or chimney, on decayed wood; main home range estimated at c. 8 ha, larger range c. 37 ha, but dependent on habitat. Usually 3 eggs, rarely 4-5, laid every second day; incubation c. 30 days, by female; chick with creamy-whitish first and second down, hazel to yellow eyes at fledging; typically, 2-3 chicks fledge at c. 5 weeks; family stays together another c. 3 months, juveniles disperse late summer to autumn. In captivity, breeds at 1 year old; in wild, age of first breeding probably at least 2 years for females, 3 for males.

Movements. Not well known; largely resident, some winter dispersal. Southernmost populations possibly partially migratory, move N and to lower altitudes in winter.

Status and Conservation. Not globally threatened. CITES II. Widely distributed and common through forest of New Guinea; moderately common on Timor; in Australia, widespread and generally common. Quite tolerant of habitat disturbance, but loss of tree hollows through clearing, degradation and lack of regeneration may cause problems in future. Some evidence of DDT-induced eggshell-thinning, but unlikely to be widespread; some evidence of secondary poisoning in pest-control programmes for rats (*Rattus*) in Australia, but local in effect.

Bibliography. Andrew (1992), Baker-Gabb (1984), Baldwin (1975), Beehler *et al.* (1986), Blakers *et al.* (1984), Bone (1995), Bravery (1970), Campbell & Rose (1996), Chatto (1989), Christidis & Boles (1994), Clancy (1977), Coates (1985), Coates & Bishop (1997), Debus (1996a, 1996b, 1997a, 1997d), Fleay (1925, 1926, 1979), Ford (1987), Higgins (1999), Hollands (1991), Hyem (1979), Inskipp *et al.* (1996), Kavanagh & Bamkin (1995), Kavanagh & Peake (1993a, 1993b), Kavanagh, Debus, Tweedie & Webster (1995), Kutt (1994), Lindsey (1992), Macdonald (1988), Mayr (1944), Mayr & Rand (1937), McNabb (1994a), Mees (1964), O'Brien (1990), Olsen (1997, 1998), Olsen & Bartos (1997), Olsen & Marples (1993), Olsen & Moon (1990), Olsen *et al.* (1993), Pizzey & Doyle (1998), Rand & Gilliard (1967), Rose (1996b), Sayers (1976), Schodde & Mason (1981, 1997), Schodde & Tidemann (1986), Simpson & Day (1998), Singor (1996), Strahan (1994), Trounson & Trounson (1987), White & Bruce (1986).

165. Morepork

Ninox novaeseelandiae

French: Ninox boubook

German: Kuckuckskauz

Spanish: Ninox Maori

Other common names: Ruru; Spotted Boobook (*leucopsis*); Norfolk (Island) Boobook (*undulata*); New Zealand Boobook (*novaeseelandiae*)

Taxonomy. *Strix novae Seelandiae* J. F. Gmelin, 1788, Queen Charlotte Sound, South Island, New Zealand.

Sometimes considered to form superspecies with *N. rudolfi* and *N. boobook*; various other proposed treatments, e.g. as member of species-group that includes *N. boobook*, *N. squamipila*, *N. theomacha*, *N. meeki*, *N. variegata* and perhaps other boobooks in Australasian Region; more research needed. Often considered to include *N. boobook* as race, but latter separated specifically by morphological and molecular differences. Race *leucopsis* formerly placed with *N. boobook*, but recently included with present species on basis of molecular affinities; possibly specifically distinct from both. Birds of North I formerly separated as race *venatica*, but differences minimal and possibly not consistent. Race *albaria* from Lord Howe I extinct. Three subspecies recognized.

Subspecies and Distribution.

N. n. leucopsis (Gould, 1838) - Tasmania and Bass Strait islands.

N. n. undulata (Latham, 1801) - Norfolk I.

N. n. novaeseelandiae (J. F. Gmelin, 1788) - New Zealand, including most offshore islands.



Descriptive notes. c. 29 cm; male c. 156 g, female c. 170 g. Very small, stocky, with relatively round wings and long tail. Indistinct greyish-white facial disc, and white or cinnamon eyebrows; upperparts chocolate-brown to deep rufous with white flecks; buff to umber flecks and streaks ventrally; golden-yellow eyes; feathered tarsi. Differs from *N. boobook* in being generally smaller and darker, with more rounded wings. Sexes similar, female slightly more streaked/spotted on head and back. Juvenile tends to be more heavily streaked than adult on crown, nape and breast. Races differ in size, and in intensity and extent of plumage colours and markings: *leucopsis* more neatly spotted white; *undulata* more barred above, more rufous below. Voice. Commonest call a repeated double hoot, "boo-book".

tent of plumage colours and markings: *leucopsis* more neatly spotted white; *undulata* more barred above, more rufous below. Voice. Commonest call a repeated double hoot, "boo-book".

Habitat. Forest, farmland and pine plantations at lower altitudes, extending up to tree-line. Roosts under dense canopy or in tree hole.

Food and Feeding. Mainly insects; also spiders, and small to medium-sized vertebrates such as birds, rodents, bats and lizards. Typically begins hunting in early hours of dusk, returning before dawn to roost. Hunts mainly by perch-hopping, snatching prey from canopy, from ground and around street lights; hawks flying insects in air.

Breeding. Lays late Sept-Nov, later in S than in N. Monogamous; territorial, intensified calling prior to breeding. Nest in tree hollow, less often in epiphytes, rarely in cave or river-bank cavity; home range estimated at 4-8 ha in New Zealand forest. Usually 2 eggs, rarely 3, laid every second day; incubation c. 30 days, by female; chick with greyish-white first down, sooty-grey second down and golden-yellow eyes; typically, 2 chicks fledge at c. 5 weeks; family stays together another c. 3 months. In captivity, can breed at 1 year old; in wild, age of first breeding probably at least 2 years for females, 3 for males.

Movements. Mainly resident; movements poorly understood. Young may disperse in winter, reaching islands where not normally seen; a few from Tasmania winter in mainland Australia.

Status and Conservation. Not globally threatened. CITES II. Widely distributed and common through forest of New Zealand's main islands and large offshore islands; also in farmland, small woods, parks and treed suburbs, and some pine plantations, but displaced by introduced *Athene noctua* in more open parts of South Island; some evidence of secondary poisoning in pest-control programmes for possums (Phalangeridae), but local in effect. Race *undulata* endangered on Norfolk I mainly through clearing and selective logging, only 1 female individual remaining in 1985-86; now survives as hybrid population *undulata* × *novaezeelandiae*, using nestboxes. Race *albata* extinct on Lord Howe I since 1950's, this due to clearing of forest and introduced species. Race *leucopsis* widespread and common in Tasmania. Race *undulata* CITES I.

Bibliography. Anderson (1992), Brown *et al.* (1998), Chambers (1989), Christidis & Boles (1994), Clark, J.M. (1992), Clark, R.J. & Mikko (1989), Cunningham (1948), Dawson *et al.* (1978), Disney & Smithers (1972), Double & Olsen (1997), Garnett (1993), Falla *et al.* (1981), Fielding (1979), Fitzgerald *et al.* (1989), Garnett (1993), Green *et al.* (1986), Hay (1986), Heather & Robertson (1997), Hermes (1985), Hicks (1991), Hicks *et al.* (1990), Higgins (1999), Hindwood (1940), Hogg & Skegg (1961), Howell (1976), Hutton (1991), Imboden (1975), Inskipp *et al.* (1996), King (1978/79), Knox & Walters (1994), Lindsay & Ordish (1964), McCann (1959), Moon (1967, 1992), Norman, Olsen & Christidis (1998), O'Donnell (1980), Olsen (1989, 1996, 1998), Olsen & Hicks (1994), Olsen & Moon (1990), Olsen *et al.* (1989), Robertson (1985), Rooke (1986), Scarlett (1961), Schodde & Mason (1981), Schodde *et al.* (1983), Sibson (1989), Smithers & Disney (1969), Soper (1976), St. Giron *et al.* (1986), St. Paul & McKenzie (1977), Stephenson & Minot (1998), Turner *et al.* (1968), Williams (1975).

166. Brown Hawk-owl

Ninox scutulata

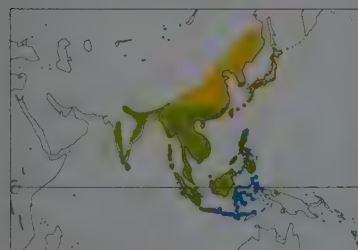
French: Ninox hirsute **German:** Falkenkauz **Spanish:** Ninox Pardo
Other common names: Brown Boobook, Oriental/Hume's/Philippine/Burmese Brown Hawk-owl, Indonesian Punggok

Taxonomy. *Strix scutulata* Raffles, 1822, Sumatra.

Relationships uncertain. Normally, 9-12 races recognized; *obscura* perhaps specifically distinct, but many others doubtfully separable subspecifically; taxonomy in need of revision. Name *scutulata* formerly applied to populations from E China, Korea, Japan and Taiwan (currently *japonica*) on erroneous supposition that type specimen, from Sumatra, was migrant form; populations now recognized as nominate form were placed in race *malaccensis*. Eleven subspecies recognized.

Subspecies and Distribution.

- N. s. ussuriensis* Buturlin, 1910 - SE Siberia, SE Manchuria and N Korea.
- N. s. japonica* (Temminck & Schlegel, 1844) - E China, C & S Korea, Japan and Taiwan.
- N. s. lugubris* (Tickell, 1833) - N & C India to W Assam.
- N. s. hirsuta* (Temminck, 1824) - S India and Sri Lanka.
- N. s. obscura* Hume, 1873 - Andaman and Nicobar Is.
- N. s. burmanica* Hume, 1876 - E Assam to S China, S to N Malay Peninsula, Thailand and Indochina.
- N. s. palawanensis* Ripley & Rabor, 1962 - Palawan.
- N. s. randi* Deignan, 1951 - Philippines (Luzon, Marinduque, Mindoro, Negros, Cebu, Siquijor, Mindanao, Basilan).
- N. s. scutulata* (Raffles, 1822) - S Malay Peninsula, Riau Archipelago, Sumatra and Bangka.
- N. s. javanensis* Stresemann, 1928 - W Java.
- N. s. borneensis* (Bonaparte, 1850) - Borneo and N Natuna Is.



Descriptive notes. 27-33 cm; 172-227 g. Medium-sized hawk-like owl with long wings and tail. Face almost wholly dark; indistinct dark facial disc, and small white patch between golden-yellow eyes; compact plumage, uniformly dark brown dorsally, tail broadly barred pale; buffish-white below, boldly streaked reddish-brown; grey bill with darker tip; feathered tarsi. Distinguished from most congeners by lack of white spots above; from *N. affinis* by brown head. Sexes similar in plumage, female larger. Geographical variation in size, colour of head and amount of white ventrally; *obscura* distinct, wholly dark brown all over. **VOICE.**

Most commonly a repeated, mellow, rising falsetto, disyllabic hoot, "pung-ok" or "oo-uk"; occasionally duets.

Habitat. Wide variety of deciduous, evergreen and coniferous forest types, from scrub to mangrove, rainforest and river thickets; also cultivated land, including plantations, parks and suburbs; in lowlands and hills, up to 1200-1500 m, but dependent on area. Roosts by day singly or in pairs under thick canopy or among creepers.

Food and Feeding. Mainly flying insects, such as dragonflies (Odonata) and moths (Lepidoptera) caught in air; also takes small crabs (Decapoda), and wide variety of vertebrates including lizards, amphibians, small birds and mammals, including bats. Crepuscular and nocturnal; begins hunting before dusk, at forest edge or in cultivated areas.

Breeding. Lays Mar-Apr in Sumatra and Sri Lanka, Mar-Jun in Assam, Apr in China, late May-Jul in Japan, c. Jul (and earlier?) in India. Monogamous. Nest in tree hole. Usual clutch 2-5 eggs, but varies regionally; incubation said to take 25 days, but this probably too short, and fledging a further 28 days.

Movements. N races migrate as far S as Malay Peninsula, Sumatra, Java, Borneo, Philippines, Sulawesi, Moluccas and Lesser Sundas, to overlap with resident tropical S populations; record of beach-washed specimen, probably *japonica*, on Ashmore Reef, NW Australia. Some Japanese birds winter in E China.

Status and Conservation. Not globally threatened. CITES II. Very common in Japan in summer; common passage migrant to Korea in Apr-May and Sept, with a few summer visitors to C & S provinces; rare in SE Siberia. Uncommon in Borneo and Sumatra; rare in Java; generally uncommon throughout Moluccas and Lesser Sundas, but slightly more common in N Sulawesi region, including Talaud Is and Sangihe. In Indian Subcontinent, locally fairly common in N; common in SE Asia.

Bibliography. Ali (1996), Ali & Ripley (1981), Brazil (1991), Brazil & Yamamoto (1989a), Caldwell & Caldwell (1931), Coates & Bishop (1997), Deignan (1945), Dickinson (1975), Dickinson *et al.* (1991), Étchéopar & Hue (1978), Flint *et al.* (1984), Gore & Pyong-Oh (1971), Grimmett *et al.* (1998), Hellebrekers & Hoogerwerf (1967), Higgins (1999), Inskipp & Inskipp (1991), Kawamoto (1991), Knystautas (1993), Lekagul & Round (1991), MacKinnon & Philipps (1993), Madoc (1976), van Marle & Voous (1988), McCann (1933), Medway & Wells (1976), Nakamura (1975), Neelakantan (1979), Phillips (1978), Riley (1938), Ripley (1982), Roberts (1991), Rozendaal & Dekker (1989), Sankaran (1998), Schodde & Van Tets (1981), Smythies (1981, 1986), Stepanyan (1990, 1995), Taniguchi (1983), Tikader (1984), Voous (1988), Wells (1999), White & Bruce (1986), Zhao Zhengjie (1995).

167. Andaman Hawk-owl

Ninox affinis

French: Ninox des Andaman **German:** Andamanenkauz **Spanish:** Ninox de Andamán
Other common names: Nicobar Hawk-owl, Andaman/Nicobar Boobook

Taxonomy. *Ninox affinis* Beavan, 1867, Aberdeen Point, Port Blair, Andaman Islands.

Affinities uncertain. Populations sometimes separated subspecifically, as *affinis* in Andamans and *isolata* in Nicobars, with third form (*rexpimenta*) on Great Nicobar occasionally separated from latter; further study, including on vocalizations, required. Monotypic.

Distribution. Andaman Is (South Andaman) and Nicobar Is (Great Nicobar, Camorta, Trinkat, Car Nicobar).



Descriptive notes. 25-28 cm. Head grey with darker eyebrows, faintly defined facial disc, white rictal bristles surrounding yellow bill; dark brown above, tail broadly barred pale; white below with bright rufous spotting or streaking, denser on upper breast; eyes yellow. Distinguished from sympatric dark race *obscura* of *N. scutulata* by pale and streaked underparts and yellow bill. Sexes similar in plumage, female slightly larger. Birds from Nicobars larger and browner. **VOICE.** Single loud "eraw" recorded in Andamans.

Habitat. Forest, rubber plantations and settlements; open forest, mangroves.

Food and Feeding. Poorly known; observed hawking moths; also takes beetles and grasshoppers. **Breeding.** Largely unknown; young bird found in May.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Andaman Islands EBA and Nicobar Islands EBA. Currently considered Near-threatened. Few records, but species reported as frequently sighted Jan-Mar 1996 at S tip of Great Nicobar. Andaman and Nicobar Is are least spoilt islands remaining in Indian Ocean; thus, species' immediate future seems secure, although long-term survival uncertain.

Bibliography. Abdulali (1967, 1978), Ali & Ripley (1981), Butler (1899), Diamond, A.W. (1985), Grimmett *et al.* (1998), Ripley (1982), Sankaran (1998), Stattersfield *et al.* (1998), Tikader (1984).

168. White-browed Hawk-owl

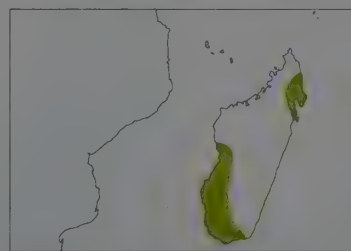
Ninox supercilii

French: Ninox à sourcils blancs **German:** Madagaskarkauz **Spanish:** Ninox Malgache
Other common names: White-browed Owl/Boobook, Madagascar Hawk-owl

Taxonomy. *Strix supercilii* Vieillot, 1817, Madagascar.

Affinities uncertain; variously considered closely related to *N. scutulata* or rather separate from entire *Ninox* genus; further research needed. Monotypic.

Distribution. NE, SW & S Madagascar.



Descriptive notes. 23-28 cm. Round, brown head with inconspicuous tan-grey facial disc, distinct white eyebrows above brown eyes; white speckles on crown; upperparts uniform brown with few white speckles, mostly on wing-coverts; underparts white with uniform brown bars throughout; yellow bill and feet. **VOICE.** Extremely vocal at night, giving 2 muffled disyllabic hoots, "ho-o-o. hoo", followed by 15-20 discordant calls, "kiang kiang...", that rise in pitch and volume.

Habitat. Open terrain with few trees, semi-arid thorn scrub, wooded savanna, deciduous dry forest, evergreen rainforest, rocky ravines; from

sea-level to 800 m.

Food and Feeding. Mainly insects; also reptiles, small birds and mammals. Strictly nocturnal. Hunts by surveying area overlooking open space from perch, and dropping to catch prey; probably relies on sight for hunting.

Breeding. Little known. Lays during Oct-Dec; nest a shallow depression on ground, or in open tree cavity; 3-5 eggs.

Movements. Resident. Rare wanderers to N Madagascar are probably dispersing immatures.

Status and Conservation. Not globally threatened. CITES II. Fairly common in W & S in dry forest, e.g. at Kirindi, Zombitse-Vohibasia National Park and Berenty Private Reserve; less common in Ankarana in N. Depends mainly on forest lands; may be at risk, since much natural habitat has been destroyed by logging. However, numbers appear to be moderately high W of central plateau and Bara region. Few reports from E side of island, but recently recorded on nest in Andranobe, Masoala Peninsula National Park, in NE.

Bibliography. Benson *et al.* (1976-1977), Dee (1986), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Kemp & Kemp (1998), Langrand (1995), Milon *et al.* (1973), Morris & Hawkins (1998), Ramanitra (1995), Rand (1936), Robertson (1995), Safford & Duckworth (1990), Sinclair & Langrand (1998).

ssp philippensis

169

ssp spilocephala

ssp spilonota

170

ssp hypogramma

ssp hantu

171

ssp squamipila

ssp forbesi

ssp goldii

ssp theomacha

173

174

175

176

ssp mono

178

ssp floridae

ssp malaitae

ssp granti

ssp roseoaxillaris

ssp jacquinoti

PLATE 19

inches 7
cm 18

177

169. Philippine Hawk-owl

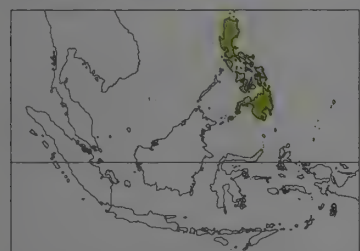
Ninox philippensis

French: Ninox des Philippines **German:** Philippinenkauz **Spanish:** Ninox Filipino
Other common names: Philippine Boobook (Owl); Mindoro Hawk-owl (*mindorensis*); Spotted Hawk-owl (*spilonota*); Mindanao/Tweeddale's Hawk-owl (*spilocephala*)

Taxonomy. *Ninox philippensis* Bonaparte, 1855, Philippines. Relationships unclear; possibly close to *N. ochracea*. Subspecific divisions uncertain and confused, and races sometimes combined into three groups based on apparent relationships: *philippensis* with *proxima* and *centralis*; *spilocephala* with *reyi*; and *spilonota* with *mindorensis*; these groups sometimes treated as three separate species. Other authors merge races as indicated by those groupings, treating only nominate, *spilocephala* and *spilonota* as valid, or with *mindorensis* as additional race; the latter, moreover, has recently been found to be quite distinct in plumage and voice, and may be a full species. Another recent proposal groups *mindorensis* and *spilonota* with *reyi*, despite the fact that latter usually allied with *spilocephala*; this new grouping of bar-bellied forms, inhabiting a considerable number of smaller islands, would include at least two unnamed races, and may constitute a separate, polytypic species, for which the name *reyi* has priority. Further research under way. Proposed race *everetti* of Siasi synonymous with *reyi*. Seven subspecies recognized.

Subspecies and Distribution.

N. p. philippensis Bonaparte, 1855 - Luzon, Polillo, Marinduque, Catanduanes, Samar, Leyte, Buad, and perhaps Biliran.
N. p. mindorensis Ogilvie-Grant, 1896 - Mindoro.
N. p. spilonota Bourns & Worcester, 1894 - Sibuyan, Tablas, Cebu and Camiguin Sur.
N. p. proxima Mayr, 1945 - Masbate, Ticao.
N. p. centralis Mayr, 1945 - Panay, Guimaras, Negros, Bohol, Siquijor.
N. p. spilocephala Tweeddale, 1879 - Basilan, Mindanao, Dinagat, Siargao.
N. p. reyi Oustalet, 1880 - Sulu Archipelago.



Descriptive notes. 15-20 cm; c. 125 g. Very small hawk-owl, with indistinct brown facial disc, greyish rictal bristles and whitish eyebrows; head and upper back dark rufous-brown, with white spotting on scapulars and upper-wing-coverts; flight-feathers heavily spotted; white throat collar; buff-white underparts streaked rufous-brown; deep orange-yellow eyes; creamy yellow-grey bill. Distinguished from *N. scutulata* by extensive white covert spots and more rufous, less chocolate-brown colour of upperparts. Sexes similar in plumage, female slightly larger. Juvenile less spotted. Races differ in coloration and markings:

spilocephala paler and less spotted above (except crown), chest washed rufous; *spilonota* barred below, with buff belly; *mindorensis* barred below, with well-marked white eyebrows. VOICE. Little known; loud, repeated, single-note "whooh".

Habitat. Secondary growth and primary forest, including remnants, gallery forest and edge, from lowlands to high altitudes. Roosts by day in darker parts of forest.

Food and Feeding. Insects and rodents.

Breeding. Nestlings in white down collected in Mar and May; nest in tree hole. No further information available.

Movements. Unknown; probably resident.

Status and Conservation. Not globally threatened. CITES II. Severe deforestation has occurred throughout Philippines, but species tolerates some degree of habitat alteration and is still locally common. Occurs in several National Parks, such as Quezon (Luzon), Mount Canlaon (Negros), Rajah Sikatuna (Bohol) and Mount Katanglad (Mindanao). Race *mindorensis* common in Siburan Forest (50 km²), the largest remnant of lowland forest in Mindoro, protected by the presence of a penal colony; more than 90% of the island, though, has been deforested, and the process has undoubtedly continued in the last few years. Races *spilonota* and *reyi*, inhabiting small islands, highly threatened by habitat destruction, with local extinctions very likely, e.g. on Cebu and Tablas.

Bibliography. Alcalá & Alviola (1970), Brooks, Dutson, Gabutero & Timmins (1995), Brooks, Dutson, King & Magsalay (1996), Collar & Rasmussen (1998), Danielsen *et al.* (1994), Delacour & Mayr (1946), Dickinson *et al.* (1991), Gilliard (1950a), Gogorza y González (1887), Gonzales (1983), Gonzales & Rees (1988), Goodman & Gonzales (1990), Hachisuka (1941), Inskipp *et al.* (1996), Manuel (1957), McGregor (1909-1910), Oliver & Wirth (1996), Parkes (1965), duPont (1971), duPont & Rabor (1973a, 1973b), Rabor (1938a, 1977), Rand & Rabor (1960), Robson & Davidson (1996).

170. Ochre-bellied Hawk-owl

Ninox ochracea

French: Ninox ocrée **German:** Ockerbauchkauz **Spanish:** Ninox Ocráceo
Other common names: Ochre-bellied Boobook

Taxonomy. *Noctua ochracea* Schlegel, 1866, Negri-lama, Gulf of Tomini, Sulawesi. Affinities uncertain. Closest relative probably *N. philippensis*; considered by some authors to be close to *N. punctulata*, but this apparently far from the case. Sometimes referred to as *N. perversa*, as name *ochracea* erroneously thought to be preoccupied. Monotypic.

Distribution. Sulawesi and Butung.

Descriptive notes. c. 29 cm. Brown upperparts and tawny underparts, with bold white scapular spots; white throat and eyebrows; yellow eyes. Differs from *N. punctulata* in paler coloration, without dark mask; from *N. scutulata* in spotted scapulars and pale throat. Sexes similar, female slightly larger. Voice. Commonest call is series of hoarse, somewhat guttural, single "kau" notes, developing into series of 2-noted calls, "wu kau", second note more drawn out than first.

Habitat. Primary and tall secondary lowland forest and riverine forest, to c. 1000 m. Roosts by day, singly or in pairs, in dense vegetation such as rattan palm.



Food and Feeding. Food apparently unrecorded. Hunts from perches in mid-storey or lower canopy, particularly where overlooking road or forest opening.

Breeding. No information.

Movements. No information. Presumably resident.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Sulawesi EBA. Little known and status uncertain; generally uncommon but locally moderately common, e.g. in Lore Lindu National Park; also occurs at Dumoga-Bone National Park and Tangkoko Nature Reserve. Fairly wide-

spread, but apparently not recorded from S Sulawesi.

Bibliography. Andrew (1992), Catterall (1997), Clark & Mikkola (1989), Coates & Bishop (1997), Holmes & Philipps (1996), Mees (1964), Riley (1924), Rozendaal & Dekker (1989), Stattersfield *et al.* (1998), Stressemann (1938a), Sujatnika *et al.* (1995), Watling (1983), White & Bruce (1986).

171. Moluccan Hawk-owl

Ninox squamipila

French: Ninox des Moluques **German:** Molokkenkauz **Spanish:** Ninox Moluqueño
Other common names: Moluccan Boobook

Taxonomy. *Athene squamipila* Bonaparte, 1850, Ceram.

Relationships unclear. Proposed treatment as member of species-group that includes *N. boobook*, *N. novaezealandiae*, *N. theomacha*, *N. meeki*, *N. variegata* and perhaps other boobooks in Australasian Region, or possibly with just last 3 of above-named species; more research needed. Formerly included *N. natalis* as race, but latter now afforded full species status based on plumage details and molecular evidence. Races are morphologically quite distinct, and there is some preliminary evidence that vocalizations also differ; more than one species may be involved. Four subspecies recognized.

Subspecies and Distribution.

N. s. hypogramma (G. R. Gray, 1860) - Halmahera, Ternate and Bacan group.
N. s. hantu (Wallace, 1863) - Buru.
N. s. squamipila (Bonaparte, 1850) - Seram.
N. s. forbesi P. L. Slater, 1883 - Tanimbar Is.



Descriptive notes. 25-39 cm. Plain brown head and mantle, with some spotting or barring on back, few spots on wing-coverts; flight-feathers and tail barred; chest rufous, rest of underparts whitish, all vermiculated dark brown; eyes deep yellow. Differs from *N. scutulata* and larger *N. connivens* in barred rather than streaked breast. Sexes similar, female slightly larger. Races vary in size and plumage: *hypogramma* very dark, with grey crown and rusty ventral barring; *hantu* rufous below, indistinctly barred; *forbesi* bright rusty-brown. VOICE. Commonest call a 2-note, repeated hoot, "wu-wu" or "ook-ook"; perhaps some variation between islands.

Habitat. Primary and tall secondary forest; selectively logged forest and forest edge in lowlands and hills; roosts in dense vegetation by day. Occurs from sea-level to 1200 m on Halmahera and Bacan, to 1400 m on Seram and 1750 m on Buru.

Food and Feeding. Mainly insects, but diet poorly known. Hunts from perches in mid-storey and lower canopy, often exposed branches or stumps; occurs singly or in pairs.

Breeding. Apparently undescribed.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Banda Sea Islands EBA, Buru EBA, Seram EBA and Northern Maluku EBA. Locally moderately common on Halmahera, Seram and Tanimbar Is. Nominant race occurs at Manusela National Park, Seram.

Bibliography. Andrew (1992), Bowler & Taylor (1989), Coates & Bishop (1997), Inskipp *et al.* (1996), Isherwood, Edwards *et al.* (1998), Isherwood, Willis *et al.* (1997), Norman, Christidis *et al.* (1998), Schodde & Mason (1997), Stattersfield *et al.* (1998), Sujatnika *et al.* (1995), White & Bruce (1986).

172. Christmas Hawk-owl

Ninox natalis

French: Ninox de Christmas **German:** Weihnachtskauz **Spanish:** Ninox de la Christmas
Other common names: Christmas Boobook

Taxonomy. *Ninox natalis* Lister, 1889, Christmas Island.

Formerly considered conspecific with *N. squamipila*, but separable on morphological and plumage details, molecular differences and perhaps voice. Monotypic.

Distribution. Christmas I (Indian Ocean).

Descriptive notes. 26-29 cm; 130-190 g. Dark chestnut facial mask, whitish brows, lores and throat, and golden-yellow eyes; upperparts rich rufous-brown with fine white spots on nape and wing-coverts and fine white bars on scapulars; underparts buff-white, densely barred rufous-brown; feet orange-yellow. Sexes similar in plumage, female slightly larger. VOICE. Typical call a repeated, double-noted hoot with somewhat clucking quality, "klu-gook".

Habitat. Dense rainforest, both tall evergreen and deciduous, on plateau and coastal terraces; less often in secondary forest. Roosts singly, in pairs or in family groups under dense foliage; tame and approachable.



Food and Feeding. Mainly large insects (especially Orthoptera, Lepidoptera and Coleoptera); also spiders. Occasionally small vertebrates such as geckos (Gekkonidae); birds, e.g. Christmas White-eye (*Zosterops natalis*); and introduced black rats (*Rattus rattus*). Nocturnal and crepuscular. Hunts into cleared areas, including those around roads and human settlements, hawking insects around lights; moves from perch to perch through forest in search of prey; takes prey from ground or canopy.

Breeding. Little known. Apparently extended breeding season, but possibly lays mainly c.

Jun-Jul; some observations indicate season Dec-Apr. Monogamous; territorial, intensified calling prior to breeding, beginning Apr. Nest in tree hole; defended territory estimated at c. 18 ha, maintained year-round. Clutch probably usually 2 eggs; incubation and length of nestling period unknown, probably similar to those of *N. boobook* and *N. novaeseelandiae*; fledglings dependent for 2-5 months or more.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES I. Widespread but confined to small, isolated Christmas I, where the only strigid; population estimated at c. 560 pairs in 1997. Listed as vulnerable in Australian national list. Probably declined by 25% since settlement and clearance of a quarter of forest during phosphate mining; much of island now protected in National Park, and mining has ceased.

Bibliography. Chasen (1933), Clark & Mikkola (1989), Garnett (1992, 1993), Gibson-Hill (1947), Gray (1981), Higgins (1999), Hill (1995, 1997), Hill & Lill (1998a, 1998b, 1998c), Inskipp *et al.* (1996), Kent & Boles (1984), King (1978/79), Norman, Christidis *et al.* (1998), Olsen (1998), Olsen & Stokes (1989), Phillips *et al.* (1991), Stokes (1988), Strahan (1994), Van Tets (1976).

173. Jungle Hawk-owl

Ninox theomacha

French: Ninox brune **German:** Einfarbkauz **Spanish:** Nínox Papú
Other common names: Sooty-backed/Chestnut Hawk-owl, Papuan (!)Jungle Boobook (Owl), Brown Owl(!)

Taxonomy. *Spiloglaux theomacha* Bonaparte, 1855, Triton Bay, New Guinea.

Relationships uncertain. Proposed treatments as member of species-group that includes *N. boobook*, *N. novaeseelandiae*, *N. squamipila*, *N. meeki*, *N. variegata* and perhaps other boobooks in Australasian Region; more research needed. Four subspecies recognized.

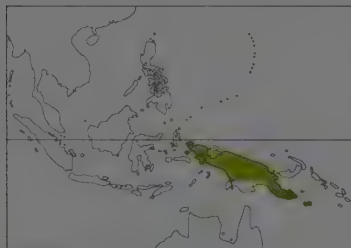
Subspecies and Distribution.

N. t. hoedtii (Schlegel, 1871) - Waigeo and Misool Is.

N. t. theomacha (Bonaparte, 1855) - New Guinea.

N. t. goldii Gurney, 1883 - D'Entrecasteaux Archipelago (Goodenough, Fergusson, Normanby).

N. t. rosselliana Tristram, 1889 - Louisiade Archipelago (Tagula, Rossel).



Descriptive notes. 20-28 cm. Small hawk-owl, relatively plain above and below. Facial disc uniformly black-brown, paler eyebrows, indistinct pale rictal bristles; sooty chocolate-brown above, unmarked or with few spots on scapulars; rich chestnut-brown below; yellow eyes; grey bill. Differs from *N. jacquinoti* in lack of white throat, dark and unbarred underparts. Sexes similar, female slightly larger. Juvenile dull brown. Races differ in size and colour: *hoedtii* duller than nominate, with browner head; *goldii* larger, belly with much white; *rosselliana* with even more white below. **VOICE.** Disyllabic "boo-boo", the two

notes identical, slightly descending in pitch, repeated every 3-4 seconds, continuing throughout most of night.

Habitat. Lowland forest, forest edge, gardens and tree groves in open country, up to c. 2500 m. Roosts under dense canopy by day.

Food and Feeding. Mainly large insects. Hunts using sallies from perch; hawks insects on wing; solitary or in pairs.

Breeding. Lays Aug; fledglings seen in Oct; eggs found in Dec in C New Guinea. Monogamous; territorial, intensified calling prior to breeding. Nest in tree hollow; usually 2 eggs.

Movements. Undescribed, probably resident.

Status and Conservation. Not globally threatened. CITES II. Widely distributed and common; occupies variety of habitats; highly adaptable.

Bibliography. Andrew (1992), Beehler (1978), Beehler *et al.* (1986), Clapp (1987), Coates (1985), Coles (1995), Diamond (1972), Gregory (1995a, 1995b), Mackay (1991), Majnep & Bulmer (1977), Mayr & Rand (1937), Mees (1965), Murray (1988), Peckover & Filewood (1976), Rand & Gilliard (1967), Simpson (1994).

174. Manus Hawk-owl

Ninox meeki

French: Ninox de l'Amirauté **German:** Manuskauz **Spanish:** Nínox de la Manus
Other common names: Manus Boobook, Admiralty (Islands) Hawk-owl

Taxonomy. *Ninox meeki* Rothschild and Hartert, 1914, Manus, Admiralty Islands.

Affinities unclear. Proposed treatments as member of species-group that includes *N. boobook*, *N. novaeseelandiae*, *N. squamipila*, *N. theomacha*, *N. variegata* and perhaps other boobooks in Australasian Region; more research needed. Monotypic.

Distribution. Manus I (Admiralty Is).

Descriptive notes. 23-31 cm. A small hawk-owl. Facial disc uniform brown, with white rictal bristles; crown and back rufous-brown, sometimes with indistinct paler mottling; flight-feathers and tail barred light rufous and brown; throat whitish or pale tawny; underparts whitish-buff with long rusty-brown streaks, densest on breast; eyes yellow; bill pale grey; feet creamy yellow.



Sexes similar, female slightly larger. Juvenile with heavier white barring above, narrower streaks below. **VOICE.** Not described.

Habitat. Forest and degraded forest. Also riparian cultivation and areas with trees around villages.

Food and Feeding. No information.

Breeding. No information.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Admiralty Islands EBA. Extremely poorly known species, with no data on population, ecology or biology; research

required. The fact that most of Manus is covered by forest (80% of vegetation being primary forest in 1987), and that this owl has been recorded in degraded habitats, suggests that, despite the tiny range, species is not currently at risk.

Bibliography. Buckingham *et al.* (1995), Coates (1985), Eastwood (1995), Gregory (1995d), Stattersfield *et al.* (1998).

175. Speckled Hawk-owl

Ninox punctulata

French: Ninox pointillée **German:** Pünktchenkauz **Spanish:** Nínox Punteado
Other common names: Speckled Boobook

Taxonomy. *Noctua punctulata* Quoy and Gaimard, 1830, Sulawesi.

Affinities uncertain; considered by some authors to be close to *N. ochracea*, but this apparently far from the case. Monotypic.



Distribution. Sulawesi, including Kabaena, Muna and Butung Is.

Descriptive notes. c. 27 cm; one male 151 g. Blackish facial disc, whitish eyebrows and throat; upperparts dark brown, densely dotted white; underparts with red-brown upper breast spotted buff, rest of underparts whitish-buff and faintly barred; yellow eyes and light creamy-yellow bill. Differs from *N. ochracea* in darker appearance, no bold white scapular spots; from *N. scutulata* in unstreaked underparts. Sexes similar, female slightly larger. **VOICE.** Most commonly a series of rising and accelerating "toi toi toi..."

notes, ending with lower-pitched "toi".

Habitat. Mainly primary lowland and hill forest to 1100 m, rarely to 2300 m; also tall secondary forest, woodland, forest edge and cultivated areas.

Food and Feeding. Almost no information on diet; one record of killing a fruit bat (*Thoopterus nigrescens*) caught in a mist-net. Forages singly or in pairs along streams in primary forest.

Breeding. Apparently undescribed; nestlings reported in Sept.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Widespread, but generally uncommon. Locally common, e.g. in Dumoga-Bone National Park; also occurs at Lore Lindu National Park.

Bibliography. Andrew (1992), van der Berg & Bosman (1986), Catterall (1997), Coates & Bishop (1997), Holmes & Philipps (1996), Rozendaal & Dekker (1989), Watling (1983), White & Bruce (1986).

176. Bismarck Hawk-owl

Ninox variegata

French: Ninox bariolée **German:** Bismarckkauz **Spanish:** Nínox de las Bismarck
Other common names: Bismarck Boobook, New Ireland Hawk-owl

Taxonomy. *Noctua variegata* Quoy and Gaimard, 1830, Carteret Harbor, New Ireland, Bismarck Archipelago.

Relationships unclear. Proposed treatments include as member of species-group that includes *N. boobook*, *N. novaeseelandiae*, *N. squamipila*, *N. theomacha*, *N. meeki* and perhaps other boobooks in Australasian Region; more research needed. Sometimes referred to, erroneously, as *N. solomonis*. New Hanover population sometimes separated as *superior*. Monotypic.

Distribution. New Britain, New Ireland and New Hanover, in Bismarck Archipelago.



Descriptive notes. 23-30 cm. Small, brown hawk-owl. Upperparts chocolate- or rufous-brown, with grey-brown head; white spotting or barring on mantle, scapulars and wing-coverts; flight-feathers and tail dark brown barred with lighter brown; underparts whitish, with dark brown or orange-brown bars; eyes yellow; feet dull yellow. Sexes similar, female slightly larger than male. Juvenile undescribed. **VOICE.** Crooning, somewhat frog-like, repeated, disyllabic "oo-oo".

Habitat. Forested lowlands, hills and lower mountains.

Food and Feeding. Presumably insects; habits little known.

Breeding. 1 newly fledged young in Apr; no other information.

Movements. Undescribed; presumably resident.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in New Britain and New Ireland EBA. No data on population, ecology or biology; studies urgently required.

Bibliography. Coates (1985), Finch & McKean (1987), Jones & Lambley (1987), Mees (1964), Stattersfield *et al.* (1998).

177. New Britain Hawk-owl

Ninox odiosa

French: Ninox odieuse **German:** Neubritannienkauz **Spanish:** Ninox de Nueva Bretaña
Other common names: New Britain Boobook, Russet Hawk-owl/Boobook

Taxonomy. *Ninox odiosa* P. L. Slater, 1877, New Britain.
Relationships uncertain; seems to be most closely related to *N. jacquinoti*. Monotypic.
Distribution. New Britain, in Bismarck Archipelago.



Descriptive notes. 20-23 cm; female 209 g. Small, finely spotted hawk-owl with conspicuous white eyebrows and throat, crown lightly dotted; upperparts chocolate-brown, sprinkled with small buff-white spots; underparts mottled white and pale brown; iris yellow to orange-yellow. Differs from *N. variegata* by smaller size, white face markings, less patterned upperparts. Sexes similar, female slightly larger. Juvenile undescribed. **VOICE.** Rapidly repeated monosyllable, "who", typically starting low, then rising in pitch, becoming faster and louder.

Habitat. Forested lowlands and hills, to at least 800 m; also in cultivated areas, plantations and

towns. Roosts by day, singly or in pairs, in canopy.

Food and Feeding. Insects and small vertebrates.

Breeding. Undescribed.

Movements. Unknown; probably resident.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in New Britain and New Ireland EBA. Appears to be quite common, but little studied; no information on numbers or on breeding biology.

Bibliography. Coates (1985), Diamond (1975), Finch & McKean (1987), Stattersfield *et al.* (1998).

178. Solomon Hawk-owl

Ninox jacquinoti

French: Ninox de Jacquinot **German:** Salomonenkauz **Spanish:** Ninox de las Solomón
Other common names: Solomon Boobook

Taxonomy. *Athene jacquinoti* Bonaparte, 1850, St George, Solomon Islands.

Relationships uncertain; probably closely related to *N. odiosa*. Subspecific divisions considered dubious by some, although most races appear fairly well defined; more research required. Seven subspecies recognized.

Subspecies and Distribution.

N. j. eichhorni (Hartert, 1927) - Buka, Bougainville and Choiseul.

N. j. jacquinoti (Bonaparte, 1850) - Ysabel and St George.

N. j. granti Sharpe, 1888 - Guadalcanal.

N. j. mono Mayr, 1935 - Mono I.

N. j. floridae Mayr, 1935 - Florida I.

N. j. malaitae Mayr, 1931 - Malaita I.

N. j. roseoaxillaris (Hartert, 1929) - Bauro and San Cristobal.



Descriptive notes. 23-31 cm. Small rusty-brown hawk-owl. Facial disc grey-brown, with thin indistinct whitish eyebrows and white throat band; upperparts rusty-brown with pale creamy-buff feather tips; breast buff-white with brown bars or spots; belly uniformly creamy; eyes yellow to orange-yellow; bill creamy-yellow. Distinguished from *N. theomacha* by barred breast and cream belly. Sexes similar, female slightly larger. Juvenile undescribed. Races vary in coloration and markings, also in size: *floridae* larger than nominate, with creamy face; *eichhorni* smaller, coarsely barred above; *mono* with

dark breast band; *granti* barred below, eyes sometimes brown; *malaitae* smallish, relatively unmarked; *roseoaxillaris* distinctive, very small, all cinnamon-rufous below with faint creamy vermiculations, axillaries pink, eyes yellow or brown. **VOICE.** Repeated single hoot, with rising inflection at end; pairs duet.

Habitat. Primary and tall secondary forest in lowlands and foothills, up to c. 1500 m. Roosts by day, singly or in pairs, in canopy or tree hollow.

Food and Feeding. Insects; probably also small vertebrates.

Breeding. No information.

Movements. No information; presumably resident.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Solomon Group EBA. Widespread within range, and apparently reasonably common. Research required on population size, ecology and breeding biology.

Bibliography. Buckingham *et al.* (1995), Cain & Galbraith (1956), Coates (1985), Diamond (1975), Hadden (1981), Mayr (1945), Schodde (1977), Stattersfield *et al.* (1998), Webb (1992).

PLATE 20

inches 7
cm 18



179



180



181



182

ssp midas



ssp clamator



183



184

ssp otus



ssp wilsonianus



ssp abyssinicus



185

ssp graueri



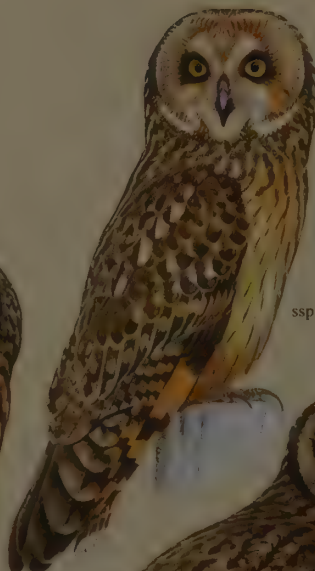
186



188



ssp galapagoensis



ssp flammeus

187



ssp bogotensis



ssp sandwichensis



189

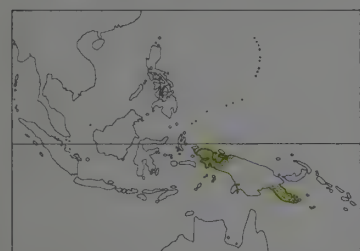
Genus *UROGLAUX* Mayr, 1937

179. Papuan Hawk-owl

Uroglaux dimorpha

French: Ninox papoue **German:** Rundflügelkauz **Spanish:** Nínox Halcón
Other common names: Papuan Boobook(!), New Guinea Hawk-owl

Taxonomy. *Athene dimorpha* Salvadori, 1874, Sorong, New Guinea. Genus closely allied to *Ninox*; sometimes merged with latter, but wings more rounded. Monotypic.
Distribution. Irian Jaya and Papua New Guinea, including Yapen I; probably occurs throughout New Guinea, but known only from NW & SE.



Descriptive notes. 30-33 cm. Small-headed and long-tailed. Whitish facial disc finely streaked black, without distinct edge, and with white eyebrows; upperparts profusely barred brown (rusty to buffy) and black; underparts light buff, boldly streaked black and brown; large bright yellow eyes; grey to black bill. Juvenile paler than adult. Voice. Undescribed.
Habitat. Lowland rainforest, forest edge and gallery forest in savanna, up to at least 1500 m.
Food and Feeding. Insects, small rodents, and large to medium-sized birds; latter include e.g. Wompoo Fruit Dove (*Ptilinopus magnificus*), 80% of weight of owl itself.

Breeding. Downy fledgling seen in early Aug. No other information.
Movements. Unknown; probably resident.
Status and Conservation. Not globally threatened. CITES II. Data-deficient. Sparsely distributed throughout range, and rarely seen; appears to be rare.
Bibliography. Andrew (1992), Beehler *et al.* (1986), Clark & Mikkola (1989), Coates (1985), Hicks (1988b, 1990), Lamothe (1993), Peckover & Filewood (1976), Rand & Gilliard (1967), Shany (1995), Weston & Weston (1973).

Genus *SCELOGLAUX* Kaup, 1848

180. Laughing Owl

Sceloglaux albifacies

French: Ninox rieuse **German:** Lachkauz **Spanish:** Nínox Reidor
Other common names: White-faced Owl(!), Whekau

Taxonomy. *Athene albifacies* G. R. Gray, 1844, Waikouaiti, South Island, New Zealand. Genus perhaps most closely related to *Uroglaux*; closely allied to *Ninox*, if not congeneric. Probably a relict species. North Island population sometimes separated as race *ruffacies*, but claimed differences in plumage often not constant and size differences possibly clinal. Monotypic.
Distribution. Formerly occurred in mainly S half of North Island in areas of lower rainfall, in South Island E of Southern Alps but well into mountains, and on Stewart I.



Descriptive notes. 38-47 cm; c. 600 g. Medium-sized terrestrial owl with broad head, short wings, long tail and long legs. Forehead, sides of head and throat greyish-white with black feather shafts; facial mask white to light rufous, obvious but with ill-defined edges; upperparts rufous-brown, streaked dark brown, and with whitish to ochraceous feather edges; scapulars and wing-coverts dark brown, streaked and spotted yellowish-white; tail dark brown, barred yellowish-white; underparts deep ochraceous, broadly streaked dark brown; bill greyish horn; eyes very dark red-brown or hazel; legs feathered pale ochraceous; toes light brown, covered with dark hairs. Juvenile undescribed. Voice. Main call a loud, repeated "coo-ee" or "kee-wee"; laughing call prolonged "cack-cack-cack".

Habitat. Rocky valleys and cliffs in open country and temperate woodland; also scrub and forest edge.
Food and Feeding. Earthworms (Lumbricidae), insects, and small vertebrates such as birds, bats, rodents, frogs and lizards. Thought to have hunted mainly on ground, also from low shrubs and lower parts of trees; probably nocturnal and crepuscular.
Breeding. Little known. Laying late Aug-Oct. Nest in dry crevice among rocks or under boulders, cavity sometimes lined with dry grass, sedges, roots, etc. Usually 2 eggs, incubated by female; chick hatched in coarse yellow-white down.
Movements. Unknown: thought to be resident.
Status and Conservation. Almost certainly EXTINCT. CITES II. Once common and widespread. Decline, rapid after c. 1880 but first noticed in 1840's, coincided with settlement by Europeans, and was probably brought about by combination of habitat change and introduced predators (mustelids and domestic cats), along with human persecution. Species often claimed to have been extinct by 1914, when last specimen found dead, but alleged sightings or auditory records persisted until as late as 1950, and egg fragments found in South Island (Canterbury) in 1960; occasional reports from Stewart I (1970's) and South Island (1980's) have not been subsequently confirmed.
Bibliography. Anon. (1982a), Blackburn (1982), Buller (1887-1888, 1905-1906), Clark & Mikkola (1989), Eck & Busse (1973), Falla *et al.* (1981), Fuller (1987, 1999), Gill (1991, 1996), Greenway (1967), Heather & Robertson (1997), Higgins (1999), Holdaway (1996), Holdaway & Worthy (1996), Kinsky (1970), Knox & Walters (1994), Marples (1946), Myers (1923), Robertson (1985), Sayers (1998a), Shuker (1993), Smith (1884), Williams (1962), Williams & Harrison (1972), Worthy (1997), Worthy & Holdaway (1994a, 1994b, 1995).

Subfamily ASIONINAE

Genus *PSEUDOSCOPS* Kaup, 1848

181. Jamaican Owl

Pseudoscops grammicus

French: Hibou de la Jamaïque **German:** Jamaikaeule **Spanish:** Búho Jamaicano
Other common names: Brown Owl(!)

Taxonomy. *Ephialtes grammicus* Gosse, 1847, Tait-Shafton, Jamaica. Formerly merged with *Asio*; later suggested that closely related to *Asio clamator* and *Asio stygius* and that all three be placed together in *Pseudoscops*; more recent DNA studies, however, seem to confirm that present species better treated in monotypic genus (see page 86). Genus believed to be possibly closest to *Asio*, with similar contact calls, but often considered particularly close to *Otus*, while some authorities think that it is linked with *Athene* and *Aegolius*. Monotypic.
Distribution. Jamaica.



Descriptive notes. 27-34 cm. Ear-tufts conspicuous; well-developed facial disc rufous, edged white and black; upperparts rufous, finely vermiculated black; breast and belly rufous with narrow dark brown shaft streaks; flight-feathers and tail short, irregularly barred dark brown; dark eyes and light bluish-grey bill; naked grey toes. Juvenile lighter above, with back light greyish-brown, rest of plumage light dull cinnamon-buff. Voice. High, quivering hoot and guttural growl.
Habitat. Open woodland, forest edge, occasionally open parkland; enters gardens. Mainly in coastal and lowland areas, rarely in mountains.
Food and Feeding. Insects, especially beetles;

also mice, lizards and tree frogs. Nocturnal.
Breeding. Season probably Dec-Jun. Nest in cavity of large tree, or in tree fork concealed by vegetation; 2 eggs.
Movements. Resident.
Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Jamaica EBA. Considered common and widespread in Jamaica; ecology, however, remains little known and population status therefore difficult to assess. Extensive cutting of forest has probably reduced its range and numbers; advisable to monitor status while island's forest areas continue to be destroyed.
Bibliography. Anon. (1998a), Bond (1985), Downer & Sutton (1990), Olson (1995), Raffaele *et al.* (1998), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Wiley (1986b).

Genus *ASIO* Brisson, 1760

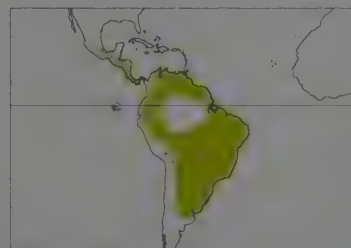
182. Striped Owl

Asio clamator

French: Hibou strié **German:** Schreieule **Spanish:** Búho Gritón

Taxonomy. *Bubo Clamator* Vieillot, 1807, Cayenne. Often placed in monotypic genus *Rhinoptynx*, which has been merged with *Pseudoscops* by some; seems, however, to be very closely related to other *Asio* species, this supported by recent DNA studies. Race *forbesi* sometimes merged with nominate. Four subspecies recognized.

Subspecies and Distribution.
A. c. forbesi (Lowery & Dalquest, 1951) - S Mexico to Panama.
A. c. clamator (Vieillot, 1807) - Colombia and Venezuela S to E Peru and C & NE Brazil.
A. c. oberi (E. H. Kelso, 1936) - Tobago and NE Trinidad.
A. c. midas (Schlegel, 1862) - E Bolivia and S Brazil S to N Argentina and Uruguay.



Descriptive notes. 30-38 cm; male 320-350 g, female 400-500 g. Long black ear-tufts; facial disc mostly white, bordered black; upperparts cinnamon-buff, finely vermiculated and heavily striped blackish; flight-feathers and tail barred sooty-brown; breast and belly buff with black shaft streaks; dark eyes and grey bill. Juvenile has cinnamon face, bordered white and lightly streaked black, body plumage buff, barred greyish. Race *midas* larger, usually paler; *forbesi* small. Voice. Single, nasal hoot lasting c. 1 second, loudest and highest in middle, "hooOOoh" or "hnnNNNhh"; female higher-pitched; also 7-8 sharp, dog-like barks, "hu-hu! how! how!", sometimes given by mates in chorus. Juvenile has slightly shrill, whistled scream, "heeeen" or "hreeeh", repeated.

Habitat. Wide variety of habitats, from sea-level to 1400 m; tropical forest, forest edge, riparian woodland, savanna, marshes, rice fields, grassy clearings, scrub, thick hedges, woodland patches, agricultural and suburban areas, and sometimes plantations. Lives alone, in pairs or in groups; roosts in groups of up to c.12 individuals.
Food and Feeding. Mostly small mammals such as rodents (*Liomys*, *Calomys*, *Rattus rattus*, *Reithrodon auritus*, *Holochilus brasiliensis*), birds such as Eared Dove (*Zenaida auriculata*) and Grey-faced Quail Dove (*Geotrygon caniceps*), reptiles, and large insects such as long-horned grasshoppers (Tettigoniidae). Hunts by quartering low over open countryside, swooping after prey; also hunts from perch, dropping to ground.

Breeding. Lays Aug-Mar, but variable: Aug in Argentina, Sept-Oct in Surinam, Dec in Panama, late Jan-Feb in El Salvador. Nest in grassy clump on ground, on flat surface at no great height, or in tree. 3 eggs (2-4); incubation period c. 33 days; usually only 1 chick fledges.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Widespread, though local and uncommon, or patchily distributed; status generally poorly known, and little information on ecology and biology. Race *oberi* little known, may even be extinct.

Bibliography. Anderson *et al.* (1998), Belton (1984), Binford (1989), Canevari *et al.* (1991), Clark & Mikkola (1989), Contreras *et al.* (1990), Fraga (1984b), Friedmann (1927), Haverschmidt & Mees (1994), Herklots (1961), Hilty & Brown (1986), Howell, S.N.G. & Webb (1995a), Howell, T.R. (1957), Kamstra (1986), King (1978/79), Klimaitis & Moschione (1987), Krabe (1981), Land (1970), Lowery & Dalquest (1951), Martínez, M.M. *et al.* (1996), Massoia (1988), Meyer de Schauensee & Phelps (1978), Monroe (1968), Motta-Júnior & Talamoni (1994), Olson (1995), de la Peña (1994), Ridgely & Gwynne (1989), do Rosário (1996), Saibene *et al.* (1996), Short (1975), Sick (1993, 1997), Slud (1964), Snyder (1966), Spicknall & Pickett (1983), Stiles & Skutch (1989), Stotz *et al.* (1996), Thurber *et al.* (1987), Tostain *et al.* (1992), Voous (1988), Wetmore (1968a).

183. Stygian Owl

Asio stygius

French: Hibou maître-bois

German: Styxeule

Spanish: Búho Negruzco

Taxonomy. *Nyctalops stygius* Wagler, 1832, Minas Gerais, Brazil.

Has been proposed that species be included in *Pseudoscops*, but recent DNA studies appear to confirm its placement in *Asio*; very closely related to *A. otus*. Populations of NW South America usually placed in *robustus*, sometimes included in nominate; races *lambi*, *noctipetens* and *barberoi* poorly differentiated, possibly not valid. Six subspecies recognized.

Subspecies and Distribution.

A. s. lambi R. T. Moore, 1937 - W Mexican highlands (SW Chihuahua to Jalisco).

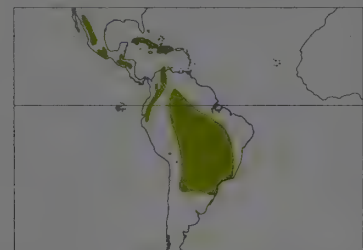
A. s. robustus L. Kelso, 1934 - from S Mexico (Guerrero and Veracruz) discontinuously to NW Venezuela, Colombia and Ecuador.

A. s. siguapa (d'Orbigny, 1839) - Cuba and I of Pines.

A. s. noctipetens Riley, 1916 - Hispaniola and Ile de Gonâve.

A. s. stygius (Wagler, 1832) - from N Brazil S to E Bolivia, NE Argentina and SE Brazil.

A. s. barberoi W. Bertoni, 1930 - Paraguay and N Argentina.



Descriptive notes. 38-46 cm; c. 675 g. Large, dark owl with prominent ear-tufts. Whitish forehead contrasts with blackish facial disc; upperparts blackish-brown, barred and spotted buff; underparts dirty buff, heavily streaked and barred dark brown; orange-yellow eyes, black bill; feet naked, toes bristled. Juvenile upperparts sooty-black, more or less mottled white or buff; underparts buff to yellow-buff, heavily spotted and streaked sooty-black. Race *robustus* paler, more spotted above; *siguapa* with markings whiter. Voice. Single deep, emphatic "bUuh", repeated at intervals of 6-10 seconds; female utters short, cat-like "miah".

Habitat. Montane pine and pine-oak forest, submontane evergreen forest, deciduous forest, humid Chaco woodland, *Araucaria*-dominated forest, *restinga* forest, parks and open areas with trees. From sea-level to 3100 m; in Mexico 1500-3000 m, in Belize 0-800 m, in Venezuela from 100 m, and in Colombia at 1700-3000 m.

Food and Feeding. Small mammals such as rodents and bats; also birds, reptiles, crustaceans and insects. Strictly nocturnal.

Breeding. Lays Nov-May. In Cuba nest found in tree, another on ground built with shredded palm leaves; as *A. otus*, will also use stick nest of other bird; 2 eggs.

Movements. Little known, probably largely resident; suspected visitor during Feb-Apr on Cozumel I, off NE Yucatán.

Status and Conservation. Not globally threatened. CITES II. Considered generally rare or patchily distributed; fairly common in W Mexico, uncommon to fairly common in Belize, rare and local in Colombia. Distribution incompletely documented. Subspecies on Caribbean islands rare and vulnerable, now confined to mountain forest; declines probably due to habitat loss, deforestation and association with ill omen. Protected in Dominican Republic, but still regularly killed in superstitious belief that it represents a witch; an education programme would benefit this species. Suffers some road casualties. Data on life history needed to develop conservation strategies.

Bibliography. Barbour (1943), Bates *et al.* (1992), Blendinger (1998), Canevari *et al.* (1991), Contreras *et al.* (1990), Dod (1992), Fjeldså & Krabbe (1990), Franz (1991), Hayes (1995), Hilty & Brown (1986), Howell & Webb (1995a), Howell *et al.* (1992), Kaufman (1997), Kirkconnell *et al.* (1994), Land (1970), Melo-Júnior *et al.* (1996), Meyer de Schauensee & Phelps (1978), Motta-Júnior & Taddei (1992), Oliveira (1981), Olrog (1985), Olson (1995), de la Peña (1994), Raffaele *et al.* (1998), Ridgely & Gwynne (1989), do Rosário (1996), Schaldach (1963), Scherer-Neto (1985), Sick (1993, 1997), Stotz *et al.* (1996), Voous (1988), Wetmore & Swales (1931), Wiley (1985, 1986b), Williams & Tobias (1994).

184. Northern Long-eared Owl

Asio otus

French: Hibou moyen-duc

German: Waldohreule

Spanish: Búho Chico

Other common names: (Common) Long-eared Owl

Taxonomy. *Strix Otus* Linnaeus, 1758, Sweden.

Forms superspecies with *A. abyssinicus* and *A. madagascariensis*, both of which have been treated as races of present species. Recent protein studies indicate unusually large genetic distance between present species and *A. flammeus*. Given nomadic tendencies of species, subspecific status of *tuftsi* questionable, possibly inseparable from *wilsonianus*. Four subspecies recognized.

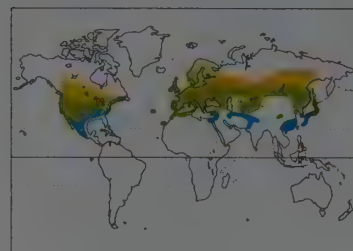
Subspecies and Distribution.

A. o. otus (Linnaeus, 1758) - Eurasia, from British Is and Iberia E to Sea of Okhotsk, S to Mediterranean islands, Middle East, N Pakistan (has bred) and Japan, with isolated population in EC China; also Azores, and NW Africa (Morocco to NW Tunisia).

A. o. canariensis Madarász, 1901 - Canary Is.

A. o. tuftsi Godfrey, 1948 - W Canada (S Yukon, S British Columbia E to Saskatchewan) S to Mexico (NW Baja California, Nuevo Leon) and S USA (W Texas).

A. o. wilsonianus (Lesson, 1830) - from SC & SE Canada (Manitoba E to Nova Scotia) S in USA to N Oklahoma and Virginia.



Descriptive notes. Male 35-38 cm, 220-305 g; female 37-40 cm, 260-435 g; wingspan 90-100 cm. Medium-sized owl with large, round head and conspicuous ear-tufts. Rounded facial disc buff, with white inner eyebrows and lores; eyes orange, bill black; upperparts a mixture of black, brown, grey, buff and white; wings long and rounded, with buff patch above and dark carpal crescent below; underparts whitish-grey and buff with dark brown streaking and barring; tarsi and toes densely feathered. Sexes similar; female somewhat darker, especially on facial disc, more heavily streaked above, darker buff on underwing-coverts. Juvenile with facial disc, wings and tail as adult, rest of plumage greyish-buffed buff. Race *canariensis* darker than nominate; *wilsonianus* also darker, with more prominent barring below, rufous facial disc, yellow eyes, *tuftsi* similar but not so dark. Voice. Complex repertoire in breeding season; advertising song of male is series of 10 to over 200 "hooh" notes, evenly spaced about 2-4 seconds apart; common alarm call a barking "ooack ooack ooack". Mostly silent at other times of year.

Habitat. During breeding season, inhabits dense vegetation adjacent to open areas such as grassland or shrubland, including open forest, from near sea-level to 2750 m; nests and roosts in forest. In Idaho, large numbers nest in willows (*Salix*), cottonwoods (*Populus*) and junipers (*Juniperus*) adjacent to shrub-steppe desert; in dense or brushy vegetation in open habitats in SW & NW USA, and in coniferous or deciduous forest near open meadows in Michigan and W Oregon. In mainland Europe, breeds in edge woodland and scrub; in Britain prefers shelterbelts, small groves and thickets surrounded by moorland, grassland, marshes or farmland. In winter range, occupies similar habitats to those when breeding, including farmland with hedgerows; often in traditional sites, using same tree groves annually. Roosts communally during non-breeding season, typically 2-20 birds but can be up to 100.

Food and Feeding. Mainly small mammals; birds important in a few studies. Voles (*Microtus*) dominate diet in many areas of North America; in N Italy, switched to birds following heavy snowfall. Nocturnal; occasionally crepuscular, usually during breeding. Hunts below canopy in open forest; active-search hunter, courting back and forth with fast wingbeats, interrupted by short glides; occasionally hovers; adaptations for silent flight well developed, including comb-like fringe on leading edge of outer 2 primaries, soft, hair-like fringe on trailing edge of remiges, and downy surface on dorsal side of remiges. Sometimes hunts from perch, especially when windy. Probably locates most of prey by ear (can capture mice in complete darkness). Most food probably captured on ground or from low vegetation. Kills small mammals by biting back of skull. Swallows prey whole; may eviscerate rodents and leave entrails uneaten.

Breeding. Season Feb-Jul; in Netherlands, laying dates significantly earlier during peak vole years. Monogamous, occasionally polygynous; solitary, also with tendency to nest in small colonies. Uses abandoned stick nest of other bird, such as Common Raven (*Corvus corax*), also accepts artificial baskets; sometimes lays in cavity in tree or cliff, or on ground; site sometimes reused, often by different individuals. Male courtship involves zigzag flight around and through nest grove using deep wingbeats interspersed with glides and wing-claps; also advertising song, which may coincide with female's nest call. 5-7 eggs, occasionally more if food abundant; replacement laid if first clutch lost; incubation 26-28 days, by female, taking only short breaks at night; male feeds female throughout; hatching with eyes closed, covered with white protopluteal down, semi-altricial; chicks leave nest after 21 days, still flightless, to reside in surrounding vegetation ("branching" stage), where they roost apart, suggesting that "branching" is adaptation to reduce predation; capable of flight at c. 35 days; in Idaho study, during "branching" period, males made 2.5 times more food deliveries than females, latter fed young until 6-5-8 weeks old, then deserted, males continued to feed young for 2-3 weeks longer. Average number of young fledged per successful nest 3-4-5 (USA), 2-8-3-2 (Europe); occasional second broods in peak vole years; annual survival for adults 69% (Germany and Switzerland).

Age at first breeding 1 year. Longevity record in wild 27 years and 9 months. **Movements.** Resident and migratory; migration poorly understood. Nomadic in response to fluctuating prey numbers in N Europe: overwinters N to C Finland during years with abundant prey, otherwise migratory in most of Fenno-Scandia and across northernmost parts of Asian range; birds breeding in Europe may winter as far S as Egypt, but largely sedentary in S Europe; Azores and Canary Is populations non-migratory. Accidental Iceland, Spitsbergen, Bear I, Iraq and Kuwait; in China, breeds in N, winters in S; Asian breeders winter as far S as N India and Indochina. Spring and autumn movements in appropriate directions in USA suggest regular migration (1 ringed in Montana recovered in Guanajuato, Mexico, having travelled 3200 km); presumably a regular migrant in N Canada; commonly winters in breeding range throughout USA and extreme S Canada; accidental Alaska, Bermuda and Cuba.

Status and Conservation. Not globally threatened. CITES II. In Europe, highest densities of up to 20 breeding pairs/100 km² across lowlands of C parts and from N France to Ukraine and S Russia (e.g. Germany 35,000-80,000 pairs, Russia 50,000-500,000 pairs), declining rapidly with increasing latitude and altitude; e.g., Finnish population estimated at only 2500 pairs; similarly, far scarcer in Mediterranean Europe, consistently below 4 pairs/100 km². Fairly common in China. Numbers appear to fluctuate with rodent populations; however, has decreased in Britain and possibly elsewhere. Recent decline and irregular distribution in Britain coincide with expansion of *Strix aluco* resulting from upland reforestation, latter being physically dominant and with similar ecological requirements; increase reported in Ireland, where *S. aluco* absent. Will nest in artificial baskets and open-fronted nestboxes; artificial structures could mitigate loss of sites from reduction in corvid numbers. State listings in USA: endangered in Illinois, threatened in Iowa, and species of special concern in California, Montana, North Dakota, Wisconsin, Michigan, Missouri, and all New England states except Maine; likely factors regulating populations include fluctuating prey numbers, high nest predation and habitat changes; may be affected by nest availability, especially where corvid numbers reduced. Decline in S California attributed to loss of riparian and grassland habitats to development; in W USA, where much of nesting habitat occurs in narrow bands along watercourses, loss of riparian woodland and isolated tree groves would be highly detrimental; maintenance of healthy riparian stands would undoubtedly be beneficial. In New Jersey, loss of open habitats to urbanization and forest succession thought to limit numbers; preservation of grassland and marshes, and planting of conifers near open habitats, considered important management actions.

Bibliography. Abel & Ritchison (1995), Alegre, Hernández & Sánchez (1989), Ali & Ripley (1981), Araújo *et al.* (1974), Baieich & Harrison (1997), Barthel (1988), Beaman & Madge (1998), Becker (1994), Belcham (1995), Berger (1992), Birrer (1993), Block & Block (1990, 1991), Bodjil (1997), Bosakowski, Kane & Smith (1989), Brazil (1991), Brazil & Yamamoto (1989a), Brown (1995), Bull & Wright (1989), Campbell *et al.* (1990), Canova (1989), Carrillo *et al.* (1989), Casini & Magnani (1988), Chmielewski (1989), Clark (1983), Coyle *et al.* (1995/96), Craig *et al.* (1988), Cramp (1985), Cyr (1995b), Dathe (1988), DeGraaf & Rappole (1995), Delgado *et al.* (1986), Diaz, Asensio & Telleria (1996), Doucet (1991), Eckert (1974), Eichépcopar & Hie (1964, 1978), Evans, D.I. & Rosenfield (1987), Evans, M.I. (1994), Fajardo & Babiloni (1996a, 1996b), Fitzpatrick (1973), Flint *et al.* (1984), Fry *et al.* (1988), Fuehrer (1997),

Galeotti & Canova (1994), Galeotti, Pilastro *et al.* (1997), Garner & Milne (1998), Gil *et al.* (1983), Glue (1977b), Glue & Hammond (1974), Goodman *et al.* (1989), Gorman (1995), Gragera (1996), Hagemeyer & Blair (1997), Handrinos & Akriotis (1997), Handwerk (1990), Hartung (1992), Hartung & Krause (1994), Heintzelman (1992), Holt (1997), Holt & Hillis (1987), Howell & Webb (1995a), Hue & Étchécopar (1970), Johnsgard (1979, 1988), Karaska (1987), Kaufman (1996), Kayser & Sadoul (1996), Kemp & Kemp (1998), Korpimäki (1987b, 1992a, 1992c), Korpimäki & Nordahl (1991), Kren (1987), Kropil (1990), Leboldinger & Tarnisien (1987), Lode (1994), López-Gordo *et al.* (1976), Lundberg (1979), van Manen (1992), Manners & Diekmann (1996), Maples *et al.* (1995), Marks (1984, 1985, 1986), Marks & Marks (1981), Marks & Perkins (1999), Marks, Dickinson & Haydock (1999), Marks, Evans & Holt (1994), Marti (1976), Marti *et al.* (1986), Martin, B.P. (1992), Martinez, J.A., Izquierdo *et al.* (1996), Mendelsohn (1996), Mikkola (1983), Moreno *et al.* (1984), Moskovitz *et al.* (1997), Murphy (1992), Nilsson (1981, 1984, 1987), Nogales & Herna (1988), Obuch (1989), Olson (1995), Overskaug & Kristiansen (1994), Paz (1987), Pessner & Hartung (1989a, 1989b), Purroy (1997), Ramos & González (1998), Reindl (1991), Roberts (1991), Rodríguez (1987), Rockenbach (1978), Rogacheva (1992), Roome (1995), Root (1988), Roulin (1996c), Rumbutis (1990), Russell *et al.* (1991), Rutgers & Norris (1972), San Segundo (1988), Scott (1997), Shirihai (1996), Simeonov *et al.* (1990), Slack *et al.* (1987), Small (1994), Snow & Perrins (1998), Stepanyan (1990), Stotz *et al.* (1996), Sudmann *et al.* (1994), Tome (1991, 1994, 1997a, 1997b, 1998), Trujillo *et al.* (1989), Tyler & Phillips (1978), Ulmschneider (1990), Veiga (1984), Viada (1994), Village (1981, 1992), Voronetsky (1987), Voous (1988), Walker (1993), de Wavrin *et al.* (1991), Wijnandts (1984), Williams (1996), Wolfe & de la Torre (1990), Wyllie *et al.* (1996), Yosef (1997), Zhao Zhengjie (1995).

185. African Long-eared Owl

Asio abyssinicus

French: Hibou d'Abyssinie **German:** Afrika-Waldohreule **Spanish:** Búho Abisinio
Other common names: Abyssinian/Ethiopian (Long-eared) Owl

Taxonomy. *Otus abyssinicus* Guérin-Méneville, 1843, Eritrea. Forms superspecies with *A. otus* and *A. madagascariensis*. Has been treated as race of *A. otus*, but considered specifically distinct on grounds of biometrics, and plumage and vocal differences. Race *graueri* sometimes considered inseparable. Two subspecies recognized.

Subspecies and Distribution.

A. a. abyssinicus (Guérin-Méneville, 1843) - Highlands of Ethiopia and Eritrea.
A. a. graueri Sassi, 1912 - Ruwenzori and Mitumba Mts in E Zaire/W Uganda, and Mt Kenya.



Descriptive notes. 42-44 cm. Head buffy, with dark brown bars, and long brown ear-tufts edged white; facial disc pale to dark buff-rufous, with distinct light grey eyebrows; upperparts brown with dark brown, buff and white vermiculations; flight-feathers and tail barred brown and buff; breast pale buff or more rufous, with thick brown, broken bars; lower belly pale buff or ivory with closely spaced brown streaks and cross-bars, giving chequered effect; eyes yellow; bill black. Distinguished from *A. otus* by larger size, chequered appearance of underparts, darker plumage, and more powerful feet and bill. Juvenile undescribed. Race *graueri* greyer overall and

slightly smaller than nominate race. **VOICE.** Deep, soft hoot, "ooo-ooooom", drawn out and rising in pitch, also "whooh"; female softer and higher-pitched; also barking call and high squeal when alarmed. **Habitat.** Open woodland and grassland with patches of cedar and oak forest, over 3000 m; in Ethiopia, also exotic plantations in similar habitats. Roosts in dense foliage, e.g. in giant heath; where food abundant, sometimes large communal roosts of up to 30 individuals.

Food and Feeding. Small mammals, including shrews (Soricidae), mole rats (*Tachyoryctes*) and rats, probably forming c. 90% of diet; occasionally takes small birds or invertebrates, usually in summer if small mammals not abundant. Stronger, larger feet and bill than *A. otus*, allow exploitation of larger prey. Strictly nocturnal; can spend up to 2-5 hours per night hunting. Hunts over open country, by quartering 0.5-1.5 m above ground; sometimes locates prey from perch; relies on keen hearing for hunting.

Breeding. Few data. Lays perches Jan-Jun; probably uses old stick nest of bird.

Movements. No information.

Status and Conservation. Not globally threatened. CITES II. Scarce to rather rare throughout range. Nominative race regularly recorded at Bale Mountains National Park, Ethiopia. Race *graueri* rare on Mt Kenya; known from only 1 specimen, but sighted in 1992.

Bibliography. Britton (1980), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Fry *et al.* (1988), Kemp & Kemp (1998), Lewis & Pomeroy (1989), Lippens & Wille (1976), Mackworth-Præd & Grant (1957, 1970), Olson (1995), Shirihai & Francis (1999), Short *et al.* (1990), Snow (1978), Tilahun *et al.* (1996), Turner (1976), Yalden (1973), Zimmerman, D.A. *et al.* (1996).

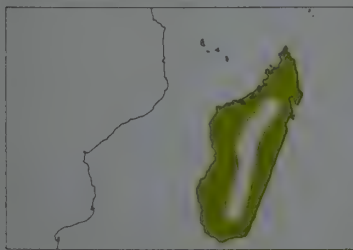
186. Madagascar Long-eared Owl

Asio madagascariensis

French: Hibou malgache **German:** Madagaskar-Waldohreule **Spanish:** Búho Malgache
Other common names: Madagaskar/Mascarene Owl

Taxonomy. *Otus Madagascariensis* A. Smith, 1834, Madagascar.

Forms superspecies with *A. otus* and *A. abyssinicus*. Has been treated as race of *A. otus*; considered specifically distinct on grounds of historic isolation, smaller size, darker eyes and more orange-yellow plumage. Monotypic.



Distribution. Madagascar.

Descriptive notes. 31-36 cm. Head dark brown, flecked with tan; long, similarly coloured ear-tufts; buffy-tan facial disc, turning to dark brown around deep, dull orange eyes; bill black; upperparts vermiculated and spotted brown, tan and black; flight-feathers and tail barred brown and buff; breast and belly light buffish with dark brown shaft streaks, becoming more widely spaced and arrow-shaped towards belly. Sexes similar, female larger. Juvenile with white down and contrasting black facial mask; ear-tufts fully visible. **VOICE.** Long series of barking "han kan, han kan" notes, accelerating and increasing in volume, dropping and fading at end; also lilting "uloooh", repeated at intervals.

Habitat. Humid evergreen forest, dry deciduous forest and gallery forest; also dense secondary woodland, including degraded habitats; observed from sea-level to c. 1600 m, occasionally to 1800 m. Roosts in thick vegetation during day.

Food and Feeding. Mainly mammals, including rats (*Rattus*) and lemurs (Lemuridae), with great proportion of diet introduced rodents; also takes free-tailed bats (*Tadarida*); occasionally reptiles, birds and insects. Long powerful claws for its body size. Strictly nocturnal. Hunts in forest and also in adjacent open areas.

Breeding. Little information. Lays Aug-Oct, perhaps in old stick nest of other bird; 3 young observed in Mar in forest area.

Movements. Resident.

Status and Conservation. Not globally threatened. CITES II. Status difficult to assess because of secretive and nocturnal lifestyle; may be overlooked. More commonly seen in E at Andapa, Maroantsetra, Sihanaka forest, Andasibe, Ranomafana, and forest of Sambirano and Montagne d'Ambre, on High Plateau; and at Morondava and Berenty in W and S. Persecuted by villagers, who regard it as an evil omen; in 1982, dead adult seen nailed up on outskirts of a village. May be threatened by deforestation, which is extensive in Madagascar.

Bibliography. Benson *et al.* (1976-1977), Dee (1986), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Goodman, Creighton & Raxworthy (1991), Goodman, Langrand & Raxworthy (1993a, 1993b), Kemp & Kemp (1998), Langrand (1994, 1995), Langrand & Goodman (1996), Milon *et al.* (1973), Morris & Hawkins (1998), Olson (1995), Rand (1936), Rasoloarison *et al.* (1995), Safford & Duckworth (1990), Sinclair & Langrand (1998), Snow (1978).

187. Short-eared Owl

Asio flammeus

French: Hibou des marais **German:** Sumpfohreule **Spanish:** Búho Campestre

Taxonomy. *Strix Flammea* Pontoppidan, 1763, Denmark.

Morphologically similar to *A. otus*, but recent studies of proteins indicate unusually large genetic distance between them. Sometimes thought to be closely related to *A. capensis*, which replaces it ecologically in Africa, but resemblance seems superficial and probably due to convergence, and vocalizations very different. Much darker race *galapagoensis* possibly specifically distinct. Race *domingensis* was formerly considered a separate species, including *portoricensis* as a race; alternatively, these two have been considered a single race of present species. Ten subspecies recognized.

Subspecies and Distribution.

A. f. flammeus (Pontoppidan, 1763) - breeds Iceland, British Is, and locally through Europe and Asia E to Kamchatka and Commander Is, S to Spain, Caucasus, NE Mongolia and NE China; also North America from W & N Alaska through Canada and S to C USA.

A. f. ponapensis Mayr, 1933 - Pohnpei I, in E Caroline Is.

A. f. sandwichensis (Bloxham, 1826) - Hawaiian Is.

A. f. domingensis (P. L. S. Müller, 1776) - Hispaniola; also (possibly this race) Cuba.

A. f. portoricensis Ridgway, 1882 - Puerto Rico.

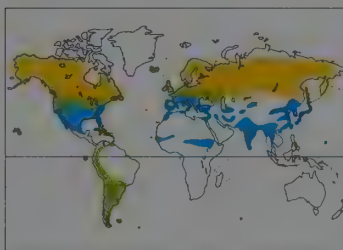
A. f. pallidicaudus Friedmann, 1949 - N Venezuela, Guyana.

A. f. bogotensis Chapman, 1915 - Colombia, Ecuador, NW Peru.

A. f. galapagoensis (Gould, 1837) - Galapagos Is.

A. f. suinda (Vieillot, 1817) - S Peru, WC Bolivia, Paraguay and SE Brazil S to Tierra del Fuego.

A. f. sanfordi Bangs, 1919 - Falkland Is.



Descriptive notes. Male 37cm, 200-450 g; female 38 cm, 280-500 g. Medium-sized owl with distinctive moth-like flight, wingbeats bouncing, high and flapping. Head large and round, with very small tufts, generally unseen, arising from centre of forehead; large, round facial disc grey-white, with black around eyes, white chin, and facial ruff and forehead white, brown and buff; upperparts mottled brown and buff, resembling dried grasses; wings long and broad, with pale ochre patch outside carpal region; central tail-feathers with brown blotching within buff area between 5-6 dark horizontal bars; underparts whitish to pale buff with dense vertical breast streaks, thinning out on sides and flanks; underwing with dark wrist markings, otherwise generally buffish-white throughout, with blackish tips; eyes yellow; bill black; thighs and feet whitish-buff. Female browner above, more buff below, more heavily streaked, larger. Juvenile has crown and rump dark brown, facial disc brown-black with feathers tipped buff, mantle with incomplete buff bars, and underparts warm buff. Races differ mainly in depth of coloration: *sandwichensis* much paler and greyer; *galapagoensis* very dark, with black face mask, streaked and barred below. **VOICE.** Generally silent, but during courtship male gives series of 13-16 notes in flight, "hoo-hoo-hoo-hoo-hoo-...", various barking calls heard in winter or during human territorial intrusion, also "kee-ow".

Habitat. Open country: tundra, marsh, grassland, savanna, moorland; also montane forest. In North America, associated with open country supporting small mammals with population cycles, such as voles and lemmings; large expanses of prairie and coastal grassland, heathland, shrub-steppe and tundra; also agricultural areas. In Europe, breeds mainly on tundra, moorland, marshes and bogs, in newly cleared forest and young evergreen plantations, in uncultivated grassland and in steppe. In China, tundra, steppe, meadows, sand dunes and marshes. Roosts primarily on ground, occasionally in trees or low bushes; in winter usually in groups. Occurs from sea-level to uplands, in Andes to as high as c. 4000 m.

Food and Feeding. Small mammals, less frequently birds. Mammals commonly include voles (*Microtus*), shrews (*Sorex*), moles (*Scapanus*), rabbits and hares (*Oryctolagus*, *Lepus*), pocket gophers (*Thomomys*), jumping mice (*Zapus*) and deer mice (*Peromyscus*), less commonly bats (e.g. *Eptesicus*) and mustelids. Birds eaten in low numbers, more at coastal than at inland sites; in analysis of nearly 10,000 pellets, 94-8% of diet mammals and 5-1% birds. Diurnal, crepuscular and nocturnal; activity probably dictated by prey density and by hunger of adults and nestlings. Hunts low above ground, often quartering with wings held in slight dihedral, or hovering and quickly adjusting flight to drop on to prey; can use auditory cues to locate prey; low wing-loading facilitates slow flight speed, aerial agility, reduced aerodynamic flight noise, ability to hear while in flight, and reduced detection by prey; can also rely on vision. In one study, of 628 foraging attempts, 21% successful, 70% unsuccessful, 9% outcome unknown. Swallows small mammals whole, or clips off head and eviscerates by pulling out trachea and oesophagus region; clips wings off birds, then swallows them whole.

Breeding. Lays Mar-Jun in N hemisphere; breeding begins Sept in S hemisphere. Seasonal monogamy, though polygamy suspected. Nest on ground; in North America in dry site with enough vegetation to conceal incubating female, often on slight ridge or mound, female scrapes out bowl and lines it with grasses and downy feathers; in Europe also dry site, sometimes in wetter situation, and female shows tendency to build nest (almost unique behaviour among Strigidae). Pair-bonding

begins late winter, male performing sky-dancing display with song, aerobatics and wing-clapping. 5-10 eggs, average clutch size 5-6 in North America, 7-3 in Europe; female incubates and broods, may retrieve eggs from outside nest by hooking bill under and rolling them back; male feeds female, and defends nest with distraction displays and vocalizations; incubation period 26-29 days; chick hatches with eyes closed, egg tooth present, with buffy down; young leave nest at c. 12-18 days, unable to fly, hide in vegetation; fledged young form communal family group and roost together during day, parents may participate at first, but sex roles and duration not known; in Europe, young not independent until 50 days after leaving nest. Hatching success variable: in Montana, of 235 eggs laid, 174 (74%) hatched, yielding c. 5-8 hatchlings/nest; in Germany, 44 (36-4%) of 121 eggs hatched from 17 nests; predation, annual fluctuations in prey density, habitat changes and catastrophic events can all contribute to wide variation in reproductive success; sometimes raises second brood. Breeding age from 1 year or less. Longevity record in wild c. 13 years. **Movements.** Thought to be highly migratory in N part of range, though migration perhaps confused with nomadic food searches and juvenile dispersal; also, wintering areas may become breeding areas if food plentiful. Although present throughout year in middle latitudes, ringing data indicate seasonal N-S and W-SW migration: bird ringed in Oklahoma recovered in Saskatchewan, 1891 km NNW; 1 ringed in British Columbia recovered 1730 km SSE in California. In Europe and Asia, migratory in N of range: N populations winter from British Is, S Scandinavia and C Asia S to N half of Africa and parts of S & E Asia; known to breed in N China and winter in S China. Accidental Spitsbergen, Bear I, Jan Mayen, Azores, Madeira and Cape Verde Is.

Status and Conservation. Not globally threatened, CITES II. In Europe, strongholds are in Scotland, Norway, Sweden, Finland, Belarus and Russia, with much smaller but locally important populations in most other countries S to Spain, Croatia and Caucasus. Best estimate of Fennoscandian population c. 12,500 breeding pairs, but highly variable depending on cycles of rodent prey; territory size may be as small as 10 ha. Much breeding in C & S Europe erratic, perhaps only when vole numbers peak or when many birds driven S from N regions by food shortages. Moorland afforestation in N Britain and elsewhere has provided ideal but temporary nesting habitat, holding abundance of rodent prey: Dutch polder reclamation had similar effect, supporting 2000-3000 owls in late 1940's, but such peaks transient. General decline through C Europe caused by drainage and intensification of agriculture, together with persecution, rodenticide poisoning, urbanization and traffic mortality. Present European total estimated at 9000-35,000 pairs, plus 10,000-100,000 pairs in Russia, where species has declined by over 50% since 1970. In North America, populations declining in many areas: considered rarest and most threatened owl in NE USA, where listed as endangered, threatened or species of special concern in 7 of 13 states; also significant declines in NW USA (parts of Idaho, Oregon and Washington). In Cuba, where formerly considered a vagrant, and in Hispaniola, dramatic increase in recent decades; now common year-round resident on both islands. Nesting habits and nomadism render species particularly vulnerable to habitat loss at any season; conversion of open habitats to agriculture, grazing, recreation, housing and resort development is a key factor in decline; reforestation in some areas may also contribute to habitat loss. Throughout range, apparently suitable habitat often not occupied, suggesting that factors other than habitat loss, probably levels of prey or predation, affect distribution and abundance. Disturbance by domestic and feral cats and dogs is known to occur; predation by skunks on eggs and nestlings suspected in decline in Massachusetts, where management suggestions have included establishing standardized survey protocol, maintaining large continuous tracts of habitat for species and its prey, monitoring predation and human disturbance, public education and research. Species has benefited indirectly from protection of nesting cover for waterfowl and from reclaimed and replanted strip-mines and dyke land, which provides nesting and foraging cover.

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188. Marsh Owl

Asio capensis

French: Hibou du Cap

German: Kapohreule

Spanish: Búho Moro

Other common names: African Marsh Owl

Taxonomy. *Otus Capensis* A. Smith, 1834, Waaipiaats, Martindale, Cape Province. Sometimes thought to be closely related to *A. flammeus*, the two replacing each other ecologically; any resemblance, however, rather superficial and probably due to convergence, and voices also very different. Three subspecies recognized.

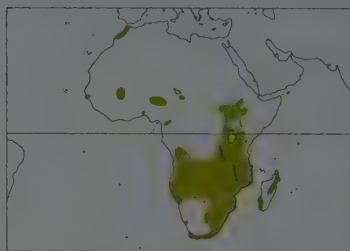
Subspecies and Distribution.

A. c. tingitanus (Loche, 1867) - NW Morocco.

A. c. capensis (A. Smith, 1834) - isolated areas in W Africa, from Senegal to Chad and Cameroon; also from S Sudan and Ethiopian Highlands, and from S Congo, S to the Cape.

A. c. hova Stresemann, 1922 - Madagascar.

Descriptive notes. 29-36 cm; wingspan 82-99 cm; 225-375 g. Round-headed, with dark areas around eyes, inconspicuous ear-tufts in centre of forehead. Uniformly brown above, except for buff tail-bars and similar buff patches in outer primaries; dark secondaries with buffy edges; dark, barred underparts; eyes dark brown; bill grey with black tip. Female larger and darker than male. Juvenile has darker facial disc



outlined in black. Race *tingitanus* darker than nominate and with rufous markings, especially on underparts, contrasting with white spotting; *hova* larger, with more distinct bars overall. **Voice.** Loud croaking "creeoww" when flushed, when circling overhead, in courtship, and on ground; also faster, repeated croaks, with female calling on higher pitch.

Habitat. Moist, coastal grassland and ephemeral marshes, up to montane grassland at 3000 m; variations in yearly rainfall continually alter habitat and distribution; may extend into dry grassland and bushveld. Sea-level to 1500 m in Madagascar.

Food and Feeding. Extremely varied diet suggests opportunist: small mammals, including bats; medium-sized mammals such as hares (Leporidae) and polecats (Mustelidae); also birds, frogs, lizards, scorpions, beetles and termites; often caches prey. Crepuscular and nocturnal. Hunts by quartering a few metres above ground with slow, steady wingbeats, alternating with short glides; may hover briefly and dive at prey; occasionally pursues on foot or aerially; hunts from perches if available.

Breeding. In N Africa lays Feb-Oct, peaking in Mar; Sept-Nov in SW Africa. Nest a shallow, unlined scrape near centre of grass tussock, often under overhanging grass; defended territory usually c. 80 ha, but pairs sometimes nest as close as 75 m, or territory as much as 2 km². Male displays at dusk, flying high with deep wingbeats and clapping wings below body. Usually 2-3 eggs (up to 6); failed early clutches sometimes replaced; female incubates and broods young, while male brings food; incubation period c. 28 days, eggs hatching asynchronously; young leave nest at 14-18 days, fledge at c. 35 days. Success higher in dry years; possibly 2 broods in years of prey abundance.

Movements. Partially migratory; wanders to uncertain extent outside breeding season. May leave areas during wet season; confirmed non-breeding wet-season visitor to coastal Gambia. Also nomadic when habitat destroyed by grass fires or drought; often local irruptions of considerable numbers with changes in suitable habitat, packing into communal roosts of up to 100 owls, though usually 15-30. Vagrants recorded in Spain, Portugal and Canary Is.

Status and Conservation. Not globally threatened. CITES II. Nominate race likely to be found where suitable habitat exists; occurs in a considerable number of protected areas throughout range. Moroccan race *tingitanus* rare within very limited range, numbers having decreased to an estimated 50-140 pairs owing to habitat changes; occurs at Merja Zerga Nature Reserve; in mid 19th century recorded in Algeria, but status uncertain and no subsequent records. Race *hova* in Madagascar uncommon and irregularly distributed. Fires during dry season destroy habitat, while grazing or thack-cutting may affect habitat quality. Nests often destroyed by fire, livestock, flooding, or predators such as mongooses (Herpestidae). Adults frequently killed by traffic, or become entangled in barbed-wire fences.

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Genus *NESASIO* J. L. Peters, 1937

189. Fearful Owl

Nesasio solomonensis

French: Hibou redoutable

German: Salomoneneule

Spanish: Búho de las Salomón

Taxonomy. *Pseudotynx solomonensis* Hartert, 1901, Santa Isabel, Solomon Islands.

Affinities uncertain. Sometimes combined with *Asio*, and usually recognized as offshoot, but more likely a primitive or relict form. Monotypic.

Distribution. Solomon Is, on Bougainville, Choiseul and Santa Isabel.



Descriptive notes. c. 38 cm. Medium-sized, robust owl with powerful beak and talons. Pale rufous facial disc, blackish around eyes, and white eyebrows; crown and upperparts dark brown, mottled rufous; flight-feathers and tail distinctly barred rufous and brown; underparts deep ochre with narrow dark brown streaks; eyes yellow, bill black; legs feathered, feet grey. Sexes similar, female slightly larger. Juvenile undescribed. **Voice.** Single drawn-out note with ghostly, mournful human quality, rising in pitch at end.

Habitat. Mostly primary and tall secondary lowland and hill forest, to c. 500 m.

Food and Feeding. Mainly phalangers, especially *Phalanger orientalis*, and possums; also medium-sized birds.

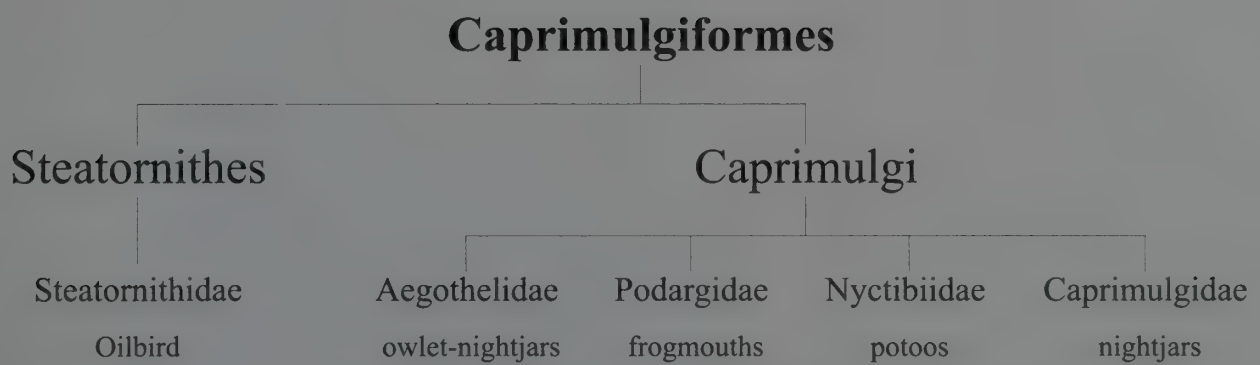
Breeding. No information available.

Movements. Probably sedentary.

Status and Conservation. VULNERABLE. CITES II. Restricted-range species: present in Solomon Group EBA. Generally rare and local, and wary of humans; thus little known. Probably threatened by forest destruction.

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Order CAPRIMULGIFORMES



Class AVES
Order CAPRIMULGIFORMES
Suborder STEATORNITHES
Family STEATORNITHIDAE (OILBIRD)



- Large nocturnal fruit-eating birds, with hooked bill, wide gape, long wings and tail, and short legs.
- 40-49 cm.



- NW South America to Trinidad.
- Roosts and nests gregariously in caves, locally from sea-level up to 3400 m; feeds in subtropical forests.
- 1 genus, 1 species, 1 taxon.
- No species threatened; none extinct since 1600.

Systematics

Alexander von Humboldt was the first scientist to see the Oilbird (*Steatornis caripensis*) in its native habitat in 1799, but he did not publish a detailed report of this encounter until 1817, and it was only much later in the nineteenth century that European anatomists received enough specimens for them to study and attempt to classify. The Oilbird's affinities to the typical owls (Strigidae) and the nightjars (Caprimulgidae) seemed clear from the beginning and were never seriously questioned, largely because of their similar plumage and nocturnal foraging behaviour. The problem was the degree of relationship to these two groups, and even, by extension, of the Caprimulgiformes to the swifts (Apodidae). A study of the pterylosis of the Oilbird suggested a close relationship with the owls, yet clearly the owl foot, used in the capture and manipulation of food, is quite different from the small leg and weak foot of the Oilbird. The Oilbird's skeleton was found to be most similar to that of the potoos (Nyctibiidae). Other anatomists have linked the Oilbird to the rollers (Coraciidae), trogons (Trogonidae) and cuckoos (Cuculidae), and Humboldt even suggested a relationship with a passerine species, the Alpine Chough (*Pyrrhocorax graculus*).

The idea that the Oilbird belongs somewhere within the Caprimulgiformes is nowadays generally recognized, and this has been supported by studies using egg-white protein. Most systematists have tended to place it next to the owls, at the beginning of the Caprimulgiformes, and it is usually believed to be an early offshoot of the order. Its closest affinities may be with the potoos and nightjars, although neither of these appears to be a particularly near relative, so the Oilbird is almost always isolated in its own family, Steatornithidae.

The fossil history of ancestral steatornithids suggests that they may have been widely distributed in a very early radiation of birds over much of the Northern Hemisphere, perhaps as early as the Paleocene. Two nearly complete skeletons from the early Eocene, about 50 million years ago, have been recovered in the Fossil Butte of the Green River Formation in Wyoming, USA. Although these fossils are smaller than the extant Oilbird, they conform closely with it in having an unusually short and stout humerus, a shortened tarsometatarsus with a weak foot and claws, a large hooked bill with a very wide gape, and a large head. These fossils, belonging to a species that has been named *Prefica nivea*, share some features with early rollers; also, they have a more primitive sternum and pelvis than does *Steatornis* and less specialized structure of the humerus, toes and tail. This suggests that the fossil form was not

adapted either for life in caves or for hovering flight, which are both distinctive forms of behaviour of the present-day Oilbird.

Most interesting is that some of the same families and even genera of angiosperm plants in the contemporary Oilbird's diet were found as fossils in the same subtropical Green River Formation. It has been postulated that the early steatornithid *Prefica nivea* may similarly have eaten the fruit and then disseminated the large seeds of these same trees (see Food and Feeding).

Another fossil related to the Oilbird was found in south-western France in the Phosphorites du Quercy, dating from the Upper Eocene to the Lower Oligocene. The French and Wyoming fossil sites of early steatornithids are remote from the present entirely Neotropical distribution, which suggests that the extant Oilbird is a relict species.

Even though it is thought that the family may have diverged from other caprimulgiforms very long ago, its relationship to them remains unequivocal. Nearly all caprimulgiforms have very short tarsi, triangular hooked bills with long rictal bristles, and wide to very wide gapes. All are also nocturnal. The Oilbird differs mainly by its exclusively frugivorous diet, since all other caprimulgiforms studied to date are essentially insectivorous.

A reasonable hypothesis may explain the fossil distribution in Wyoming and France, compared with the family's present distribution in north-west South America, stretching north to Panama and east to Trinidad and Guyana. North American climatic changes in the Pleistocene could have forced ancestral steatornithids to migrate south following the retreat of their food trees, and on into South America after the Central American landbridge was formed. There they would have lived during the fluctuating climate of the late glacial periods. However, sequences of more favourable (wetter) and less favourable (drier) climatic conditions that prevailed in South America at that time affected the forest habitat, including the fruiting trees on which the Oilbird is totally dependent. Possibly during times of less favourable conditions some population segments became isolated. This would have reduced normal gene flow, and could have created the genetic bottleneck which researchers have identified in the present-day Oilbird. Alternatively, the homogeneity of genes could be a result of the Oilbird's capacity for far-ranging dispersal (see Movements).

Morphological Aspects

The Oilbird is a large chestnut-brown bird of 40-49 cm, weighing 350-485 g, and with a wingspan of more than a metre. The female

With its legs and swift-like pampodactyl feet placed well forward, the Oilbird has a rather cumbersome, top-heavy look when perched. The species shows the typical dull, cryptic plumage of nocturnal birds, though this is punctuated with well-marked white spots along the leading edge of the wing that may help the birds to detect one another when they are flying around in poor light conditions, as is their wont.

[*Steatornis caripensis*,
Páramo de Tamá, Táchira,
Venezuela.

Photo: Juan Manuel
Renjifo/Animals Animals]



is slightly smaller than the male. The male is a greyer, slightly darker brown, whereas the female is paler and more rufous. Some birds have a greyish flush or sheen on the upperparts, while all are paler brown below. The underparts are speckled with white diamond-shaped spots, finely edged black, these spots being smaller on the throat and becoming larger toward the vent; in addition, there are small diamond-shaped spots on the head and, in some birds, on the uppertail-coverts. The Oilbird has ten primaries, twelve secondaries and ten rectrices; these feathers are also chestnut, but some are darker brown and, to a varying degree, most are banded with blackish lines broadly edged with a black speckled area.

Most outstanding are rows of large white spots which occur on the outer two primaries, the outer two secondaries, and the outer two tail feathers on each side. The carpal edge of the wing is white, and a highly conspicuous line of large white spots is found on the upperwing-coverts. All of the spots are further accented with blackish edging. In faint nocturnal light these white spots would give each bird highly visible warning lines, especially on the long wings. The Oilbird's wing bones are reported to be quite thin for the size of the bird, so the business of avoiding collisions with other conspecifics could be particularly important. Visually outstanding warning lines might be all the more advantageous to a large bird that forages silently in close groups at clumped fruit in trees at night (see Food and Feeding). Other social nocturnal-flying birds, such as migrating warblers, do not need to fly so close together and generally fly roughly parallel to each other.

The Oilbird's feathers are soft, as in most night-foraging birds, but not so silky and soft-edged as in either the Strigidae or Caprimulgidae, families of birds that depend on silent flight to catch living prey. Oilbirds can fly very slowly, hover, and turn and twist with agility, all of which contribute to their ability to manoeuvre within the narrow passages of caves. In flight at night in the open, the silhouette has been described as falcon-like, and birds have been reported sometimes to dive down like falcons with their wings half closed.

Distance flight speed has been reported to be 20-25 km/h, not very fast. The main importance of flight speed for the Oilbird is that it would limit how far a bird could fly in a single night, still making enough round-trips from fruiting trees to feed nestlings in caves.

Like vultures, Oilbirds have deep wingtip slotting to reduce stalling speed, and the wing is deeply cambered to give it lift at low speed. The birds have low wing-loading (body weight to wing area), and a low aspect-ratio (wingspan to wing width). These features are aerodynamic advantages for flying slowly, and for carrying heavy loads such as a stomachful of large-seeded fruits. The plum-

age structure and its particular modifications to allow slow hovering at fruiting trees have been suggested as pre-adaptations to ledge-nesting and ledge-roosting, where hovering is also important. Echolocation, for which the birds are famous, is used only in dark caves, and may be a more recent adaptation (see Voice).

The tail is long and graduated, with unstiffened feathers. An unusual tail arrangement, which involves its being held in an inverted V with the outer rectrices lower, appears to be another adaptation for hovering at fruiting trees, and also probably when approaching nests and roosting ledges. Oilbirds watched feeding in Peru were described as rhythmically elevating and depressing the tail, as some hummingbirds do when feeding: the downward movement of the inverted V-shaped tail generates lift, while the upward movement meets with relatively little air resistance.

The very short unscaled tarsus has a few bristle-like filoplumes. The legs are set far forward, and when the bird is perched on its nest or on an adjacent shelf in a cave, it appears to tip awkwardly forward. The anisodactyl foot has three toes pointing forwards with the hallux at a right angle to the middle toe; in the past, the Oilbird's foot was erroneously reported to be pampodactyl, like that of swifts (see page 391), with all four toes pointing forwards. The Oilbird's toe arrangement and flexible tail do not permit it to perch scansorially like woodpeckers, or to cling firmly to vertical surfaces like swifts, although it will occasionally cling briefly to cave walls. It does, however, aid nestlings, that fall or get pushed over the edge of a nest, to claw their way back to safety using the feet, bill and wings. On nests and ledges, the birds can shuffle about, but a single foot seems too weak to support the bird when it scratches its head without the support of one or both wings against the substrate.

The bill, although wide and triangular at the base, is thin and hawk-like toward the tip. On each side of the bill are 10-12 long (3-5 cm) rictal bristles, or vibrissae, directed forward and probably aiding the birds tactilely in both fruit selection and nest attendance, all aspects of which are commonly performed in the dark. The gape is very wide and can accommodate fruits of more than 6 cm in diameter. The upper mandible has a single notch, presumably as an aid in grasping and pulling off large fruits from trees. The Oilbird has a double bronchial syrinx, as in both owls and nightjars.

As soon as an Oilbird flies out of its cave it uses its eyes because the sonar, or echolocation clicks, stop abruptly. In addition to its special adaptations to the dark, the Oilbird may have good night vision. The eyes are brown, not blue as reported by Humboldt, an error that has lingered in the literature, but when spotlighted they appear bright red, as can be seen in many flash photographic pictures. Both above and below the eyes are rows of stiff bristles.

The Oilbird has an enlarged and heavily innervated olfactory organ, with very thick mucous membranes, and a nasal chamber conformation particularly adapted to carrying an airstream to these membranes. This highly developed olfactory morphology is assumed to give it a keen sense of smell, a rare feature in the class Aves that is found, for example, in kiwis (Volume 1, page 104), some petrels (Volume 1, page 218), and cathartid vultures (Volume 2, page 27), all of which also have olfactory adaptations to particular environmental circumstances. Many of the fruits that the Oilbird depends on have a highly aromatic odour (see Food and Feeding). Also, the slightly musty odour of the birds themselves has been suggested as a possible aid in individual recognition. The Oilbird has a bare oil-gland that is relatively large in relation to the bird's mass, as compared with those of both owls and nightjars.

Moult in the Oilbird has been little studied due to the difficulty in tracking individual birds, and the subsequent disturbance that handling causes to breeding birds. Nevertheless, D. Snow found that Oilbirds, like most birds, moult following breeding. Primary moult is exceedingly slow, and frequently lasts into the next breeding season; indeed, there is even some evidence that birds may begin a second primary moult before the first is completed. The moult is generally outwards from the innermost primary, but several birds were found moulting primaries from two different centres. Some moult takes place in every month of the year.

Habitat

Caves used for breeding and roosting in are considered to be the main population-limiting resource. However, it is also becoming increasingly clear that the forests used by the birds for their foraging may prove to be the more seriously threatened asset.

The Oilbird is found only in the Neotropics, from sea-level up to 3400 metres. In Trinidad and Venezuela a few sea caves have roosting and breeding populations, but these caves are not far from rich hill forests, the source of food. The combination of acceptable fruit trees and suitable caves within nightly commuting distance is not common. Apparently lacking enough truly deep, dark caves in some places, Oilbirds will roost and breed in narrow, semi-dark gorges and shallow grottos that have suitable rock shelves. One such well-known site is at Spring Hill near Arima, Trinidad, which is a water-worn tunnel with ledges only 3-4 m above a small stream. Similar places have been found at remote Venezuelan, Colombian and Ecuadorian sites with small Oilbird populations. An early suggestion that Oilbirds were associated with water is probably because most caves are found in karst, where water has hollowed out the rock, and usually there is some, or much, water still flowing through these caves.

Oilbird caves have been found in Colombia, Ecuador, Peru and Bolivia, as well as Venezuela, Trinidad and Guyana. However, individual Oilbirds have also been recorded from Brazil, Panama and the islands of Aruba and Tobago, and even as far north as central Costa Rica. Two things may account for this: first, Oilbirds fly far in a single night in search of fruiting trees; and, second, the national borders between Panama and Colombia, and those separating most South American countries are poorly explored, often rough mountainous areas, which may still harbour unknown caves.

In the most extensive caves, with large populations of thousands of birds, such as the cave at Caripe, Venezuela, the floor is covered with mounds 1-3 m high of seeds regurgitated by generations of Oilbirds. Many of these seeds germinate in the moist atmosphere, are blanched pale yellow and white, and die due to the lack of sunlight. These cave floors are alive with fauna such as spiders, cockroaches, whip scorpions, and cave crickets. Many caves, especially large ones, are also shared with thousands of bats.

Within caves, Oilbirds nest on the highest suitable ledges, often in remote sections, and sometimes as far as 770 m from an exterior opening. Since nestling Oilbirds have been harvested for centuries by indigenous peoples throughout their range, it is probable that the birds have retreated over time to the least accessible nesting and roosting areas (see Relationship with Man). Some caves, generally smaller ones, are used only for roosting and not for breeding.

General Habits

Extreme gregariousness influences all aspects of Oilbird life. The birds breed and roost closely together in gatherings of up to many thousands in suitably large caves, but also in groups of less than ten in small or marginally appropriate caves. There is great synchrony in Oilbirds' crepuscular departure from caves to nocturnal feeding grounds, and this is no doubt aided by vocalizations and perhaps by their unique echolocation clicks. At dusk there is often an hour of restlessness inside the cave when birds fly about calling and clicking, before large numbers leave the cave. Pairs, and associations of adjacently nesting pairs, return at the same time to feed nestlings several times nightly. Most other nocturnal birds feed independently on mammals and insects, but Oilbird associations are thought to be advantageous in finding and tracking ripe fruit of their preferred trees that are scattered over vast mountainous areas.

Oilbirds are strictly nocturnal, and spend the daylight hours hidden away in the depths of their dark caves. Due to the darkness, and also to the inaccessibility of most nesting and roosting sites, the birds' behaviour at the roost is rather poorly known, and these difficulties are accentuated by the fact that any human intrusion to one of the caves is almost certain to disturb the birds. As if these difficulties were not sufficient, the caves are often unhealthy sites for humans to spend much time in (see Relationship with Man).

There is an interesting case of parallel or convergent evolution between Oilbirds and some *Aerodramus* swiftlets, such as the famous edible-nest species. The two groups share no recent ancestry, and the swiftlets are confined to the Old World, occurring mainly in the Oriental Region. Both the Oilbird and the Edible-nest Swiftlet (*Aerodramus fuciphagus*), for example, nest and roost on ledges in caves, where they use echolocation for navigation (see page 399). Both species have other loud calls and screams, perhaps because there is natural loud noise in these environments such as running water or breaking ocean waves. In addition, Oilbirds and swiftlets hold their nests together with saliva, have protracted incubation and fledging periods (90-125 days for Oilbirds, up to 75-90 days for some swiftlets). Finally, the birds are highly social, and both have suffered long from persecution by man. Needless to say, much of this convergence may be ultimately attributable to their occupation of dark caves.

Voice

Any disturbance in an Oilbird cave causes a cacophony of nearly deafening shrieks, demonic screams and snarls, amplified by reverberations inside the cave, as the birds circle overhead. Humboldt called this noise "ear-splitting". These loud and intimidating vocalizations, representing a form of mobbing, are described by others as loud, harsh calls with a guttural quality and raucous screeches. A fast series of staccato sounds of many different frequencies and long sustained calls may make it easier for other birds to detect the position of calling individuals in total darkness.

The famous clicks of echolocation are used when Oilbirds fly in pitch darkness, to avoid collisions with other birds and with the walls of the cave itself. Echolocation clicks are actually sonar, because the bird judges from the echo how close it is to an object. The clicks sound like castanets, and are of a low frequency of about 7000 cycles/second, thus being audible to the human ear. Bats use echolocation to find flying food, but it is of much higher frequencies not audible to humans. The duration of Oilbird clicks is about 1 millisecond, and they are given in short bursts of 2-6 clicks repeated an average of 2-6 milliseconds apart. Experiments using adult Oilbirds flying in a totally dark room showed that they easily avoided hitting the walls and ceiling using echolocation, or when the room was lit and they could use their eyes. But in the dark, with their ears plugged they could not avoid collisions until their ears were unplugged again. Other experiments have shown that an object 20 cm in diameter is about the smallest that an Oilbird can detect by echolocation.

Outside their caves at night Oilbirds make shorter, less harsh "karr, karr" or "kuk, kuk" vocalizations, thought to be contact calls between individuals. D. Snow watched Oilbirds feeding at night, when two or three birds circled around each other with

The Oilbird is unique among birds in being a nocturnal frugivore. While in the darkness of its caves, it navigates by means of echolocation clicks, but once outside it apparently depends on sight and possibly smell in its search for fruiting trees.

Birds will travel surprisingly long distances, though when breeding they regularly return to feed their nestlings several times each night. The Oilbird's brown eyes often show up as bright red in flash lights.

[*Steatornis caripensis*,
Asa Wright Nature Centre
caves, Trinidad.
Photo: M. D. England/
Ardea]



low, clucking calls and a long, harsh "karrrr". He believed this group, and other evenly spaced trios of circling birds, might be involved in pair formation or courtship behaviour.

Chicks, while still in the egg, make high-pitched cheeps, and after hatching produce a variety of sounds, which become increasingly louder when they are begging. By the time they are well feathered, at about day 70, they utter harsh screams when alarmed, in the same way as the adults.

Food and Feeding

The Oilbird is an obligate frugivore. At night, when the birds emerge from caves they fly directly in search of fruiting trees. There, while hovering briefly, they tear fruits off the trees and swallow them whole. Nearly all of these fruits have single, usually large seeds. The muscular action of the Oilbird's stomach then strips the thin outer flesh (pericarp) from the seed, which is regurgitated intact, except in the case of figs (*Ficus*), an atypical food whose small seeds can be found in faeces.

The food of Oilbirds has been studied in Trinidad, Venezuela and Ecuador, and a total of 147,500 seeds from more than 80 species of tree have been identified. For these studies, the seeds, mostly 1-6 cm in diameter, were typically collected in wire baskets fastened underneath breeding ledges, or in Ecuador, by sampling the first 30 cm of the 2.5 m piles below nest ledges. This has afforded unusually good opportunities to identify the fruits fed to nestlings and also eaten by adult birds over the breeding season and, in Trinidad, throughout the year.

In Trinidad, D. Snow identified more than 36 species of fruit, and he found that Oilbirds fed mainly on three families: Arecaceae 52%, Burseraceae 25%, and Lauraceae 23%. In Venezuela, with a somewhat different climate, 40 species of fruit were found in the Oilbird's breeding-season diet, with proportions of Lauraceae 51%, Arecaceae 31%, and Burseraceae 7.6%. In undisturbed forests it is difficult to find flowering trees, which are often necessary for the identification of some difficult genera, so a few seeds in all studies remain unidentified.

Fruiting in many of these tropical trees is strongly seasonal, although in some species it varies from year to year, and at least one tree species used was found to be a biannual fruiting species. Generally laurel and incense trees produce abundant seasonal fruit crops, while the palms have smaller amounts of fruit but this tends to be available all year. Analysis of the most frequently selected fruits showed that the pericarp which is non-succulent is high in proteins and fat. Comparison of seeds dropped in differ-

ent Trinidad caves showed that the birds in one cave apparently exploited traditional feeding areas different from those used by the birds of other caves. Furthermore, individual birds may have special preferences. Seed collections from below active nests revealed that more tree species had ripe fruit during the months of maximum nestling feeding.

Except for palm fruits, Snow found that nearly all of the fruits that Oilbirds ate or fed to nestlings are spicy or aromatic when ripe, and a similar conclusion was also drawn by B. Tannenbaum and P. H. Wrege in their Venezuelan study. Interestingly, Snow found a species of odourless laurel fruit that was available at the same time as two other frequently eaten laurels. Analysis showed it was almost equally nutritious, but it was virtually absent from his seed collections. Thus, there is a strong case for the hypothesis that the birds find much ripe fruit by odour, which would tie in with the particularly well-developed olfactory organs (see Morphological Aspects).

The birds forage on canopy fruits from trees and palms that are 5-20 m high, though rarely they will also feed from the understorey. Groups of up to 20 or more birds circle or hover silently near a fruiting tree. Then with rapid, shallow wingbeats they fly into the foliage briefly, pluck and swallow fruits, and fly a short distance away, often returning subsequently to a different spot on the same tree. E. de Bellard noted that feeding Oilbirds settled in trees when clouds covered a bright moon, but began feeding again when the clouds had passed. Snow suggested that Oilbirds may also locate fruiting palms by sight because of the distinctive palm shape; their fruits are without noticeable odour.

At the large Caripe cave in Venezuela, R. L. Roca used radio-telemetry to follow ten adults, including birds of both sexes. Individual marked birds left the cave at the same time each night, along with hundreds of others. Although the colony as a whole appeared to forage at random each night close to the cave, single birds constantly chose to forage in the same directions and repeatedly in the same patches. The Oilbirds exploited discrete areas of primary forest and avoided disturbed forest. Most foraging was within a radius of 40 km of the cave but some birds flew as far as 150 km away in a single night.

Over time, one radio-tagged bird used a range of 85 km², while another used 96 km². One male was apparently a floater which visited the colony briefly several times then was absent from the radio signal area for periods of several weeks to two months. During the breeding season, April-July, the members of the Caripe colony together used about 300 km², but later their home range expanded to 1350 km², as fruit availability decreased. This wider area included the large area of primary forest at Mata

de Mango to the east, and still further away the extensive floodplain of the Orinoco Delta (see Status and Conservation).

Although the Trinidad birds used their caves all year, roosting in them after breeding, there was a marked post-breeding exodus from the Caripe cave. This same behaviour was postulated by B. K. Snow for the caves she investigated in Ecuador, where numbers of birds in the post-breeding period were dramatically lower than earlier in the season. These differences suggest that ripe fruit near some caves was not sufficient to support the birds following breeding, especially when fledglings increased the size of the local population.

All three of the principal Oilbird food families, and even two genera of laurels, plus three other families of fruit eaten occasionally by the extant Oilbird species, were found at the Green River Wyoming fossil site. S. L. Olson suggested that because early steatomithids "would have been effective disseminators of large angiosperm seeds, rapid co-evolution of both seed plants and their avian dispersal agents at the beginning of the Tertiary is likely".

Breeding

Everywhere that the Oilbird has been studied, it has been found to initiate breeding at the end of the dry season, although there is some variability from year to year probably due to differences in the timing and volume of rains. A typical breeding effort takes from four to more than five months, a considerable time, and this does not include post-fledging care, about which almost nothing is known.

Oilbirds appear to be monogamous on a long-term basis. Partners regularly roost together, and during breeding the off-duty bird typically perches close beside the nest, while courtship allopreening at the time of egg-laying may strengthen the pair-bond. All nesting responsibilities are shared, including nest building, incubation, brooding and the feeding of nestlings. This apparent long-term monogamy may be linked with a shortage of suitable nesting and roosting sites that appears to be the norm in most caves. Certainly some pairs repeatedly use the same nest over several years, and one ringed adult always returned to the same nest for at least 12 years.

Nests are situated on cave ledges and shelves close to the cave ceilings, sometimes 20-30 m high, though rarely as low as 4 m above the ground, and they are occasionally very deep inside caves. As pairs re-use the same nests each year, only a minor amount of reconditioning of the top nesting cup is required. These traditional nests are hard, truncated cones 20-45 cm high and 25-38 cm wide at the top. They are made of concentric layers of

regurgitated seeds, some excreta, and fruit pulp, all held together with the birds' saliva. Because the same nests are used again and again they gradually increase in height. At the top, a thin vertical rim of 2-3 cm surrounds the shallow nesting cup. In one case, F. Ortiz-Crespo described six nests in a very shallow cavity, set in a circle with the bases touching.

Some eggs are laid as early as March and as late as July in Trinidad, with the main period of egg-laying falling in April and early May; there, the clutch is of 2-4 eggs. In contrast, the main egg-laying months in Venezuela are May-June, and the clutch consists of 1-3 eggs. Eggs tend to be somewhat spherical, like some owl eggs. Ten eggs averaged 41.7 x 32.7 mm and the mean weight of ten Trinidad eggs was 20.2 g (17-22.5). Although the eggs are white they quickly become stained in the nest.

Egg-laying intervals are variable but long, at 2-9 days, and incubation begins with the laying of the first egg, so hatching is highly asynchronous, each egg hatching after 32-35 days. Some females incubate slightly more than males. As mentioned above, the non-incubating bird, when not foraging at night, remains perched alertly beside or even on the nest. Experiments showed that Oilbirds have a poor sense of egg retrieval if an egg is accidentally moved.

There is great synchrony of egg-laying within subsets of each colony, which is thought to facilitate the social foraging of off-duty birds. Pairs of birds with young return together to feed them, and at the same time neighbouring nesters also return to feed their young. During the 12-hour night very small young are fed 5-6 times, but larger young only 3-4 times.

As the diet of nestlings is entirely frugivorous, this results in slow and protracted development. Hatchlings weigh 12-16.5 g and, except for some sparse pale grey down on the underparts, they are entirely naked. At about three weeks old, they are covered in dense dark down. Also at about this time, nestlings begin to thermoregulate and are no longer brooded, and they also begin self-preening. A second generation of darker grey down pushes out the first down feathers, except for some of those on the underparts. Adult-style feathers begin erupting from sheaths on the tail, secondary coverts and scapulars by day 35, and at around ten weeks old the nestlings look similar to the adults, though they are about 50% heavier than the average adult weight of about 410 g. There is no juvenile plumage and nestlings never develop other juvenile visual signs even on the head or the bill, probably because they are raised in darkness.

Nestlings are fed entirely by regurgitation. Young birds squeal and call when an adult returns to the nest. Then the parent leans down with open bill and the chick places its bill inside. The two birds are often linked in violent struggles while fruit is transferred. Nestlings as young as 12 days old are fed whole undigested



Oilbirds almost invariably nest and roost in caves, though in places they will also utilize narrow, dark gorges. Nests tend to be placed on ledges high up the walls, preferably in remote sections of the cave, clearly with the aim of reducing the risk of predation. The nest is a truncated cone formed of regurgitated seeds and other waste products, cemented together with saliva; as the same nest is used year after year, it keeps growing taller.

[*Steatornis caripensis*, Asa Wright Nature Centre caves, Trinidad. Photo: M. D. England/Ardea]

Oilbirds are highly gregarious, roosting, nesting and feeding in the company of conspecifics, and their dense colonies are indeed noisy places, especially when disturbed by human intrusion.

As a result of their frugivorous diet, the chicks grow rather slowly and the nestling period is consequently long, but by the time they are about ten weeks old, they are much heavier than the adults. It is these deposits of fat, so attractive to humans for culinary reasons, that have given the bird its English and scientific names.

[*Steatornis caripensis*,
Asa Wright Nature Centre,
Trinidad.
Photo: Luiz Claudio
Marigo]



fruits and are able to regurgitate the seeds. Apart from these feeding bouts, the young are very lethargic in the nest.

Once a nestling is 1-2 months old, it receives nightly feedings equal to a quarter or a third of its body weight. Most fruit-eating birds eat large volumes, and the fruit is generally high in water and passes through the bird quickly, but the fruit fed to nestling Oilbirds is processed very slowly: plastic markers that researchers fed to nestlings averaged more than six hours in the birds' guts.

There is great variability in the development of nestlings of the same age, but at about 70-80 days they begin to lose their excess fat, while their plumage matures. At this same time the feeding rate decreases. Whether this slowing in the feeding rate is deliberate on the part of the adults, or a result of seasonal decrease in available fruits near the caves is not known; it may well turn out to vary from place to place.

The nestlings are brooded constantly for their first 25 days or so, at which point they are able to thermoregulate. D. Snow suggested that the extraordinary nestling fat aids the birds in thermoregulation when they are no longer brooded in dark and often wet caves, although the fact that the fat is concentrated on the chicks' ventral surface is perhaps something of an obstacle to this view.

Because of the asynchronous hatching, the growth of younger nestlings always lags behind that of their older siblings, and Tannenbaum and Wrege observed heavy brood reduction at the Caripe cave in a year of presumed fruit shortage. Oilbirds typically fledge at 100-115 (88-125) days old, after their weight has dropped close to the average adult weight and their wing feathers have attained adult length. A few ringed fledglings returned to their nests by day over a short time, but most were not found again in their natal caves.

Nearly 60% of the young that hatched in the Trinidad study reached the flying stage, so an average of a little more than 2 young were reared annually by each pair; at the Caripe cave 1.7 of the hatched young fledged. Some losses occur when eggs or young fall out of nests. In Trinidad, the crab *Pseudothelphusia garmani* was thought to be the cause of the death of some young nestlings. Venezuelan studies found that the spiny rat *Proechimys urichi* stole eggs and ate young, particularly those that fell to the cave floor. There, the highest, most inaccessible nest ledges suffered fewer losses. Predation by man at the time of maximum chick weight, for oil, appears to be the most widespread cause of nesting failure (see Relationship with Man).

The Trinidad study found that the birds renested following early loss, and that in a few cases second nests were made by early successful pairs. A few replacement nests were reported in Venezuela, but no second nestings, which perhaps corresponds with the smaller clutch there. It has been suggested that in Venezuela, and perhaps also in the Ecuador study area, the available ripe fruit within energetically economic flight range of breeding caves may limit the breeding season at those sites.

Movements

Although radio-tracking in Venezuela was used to monitor nocturnal behaviour of Oilbirds for seven months, it can not be used to track individual birds over longer time. Apparently, fledglings disperse from their caves of origin, and they are not philopatric in either Trinidad or Venezuela. Adults in Trinidad, however, continue to roost on their nests all year, where one ringed individual there was found to be faithful to the same nest for over 12 years. Nevertheless, at the Caripe cave in Venezuela there is usually a strong post-breeding departure to the Mata de Mango forest area east of the cave. In that area there are numerous smaller caves that are suitable for roosting, but apparently few that are adequate for breeding, and after the breeding season the forest there has more fruit (see Status and Conservation). The difference between these two tendencies may be that in Trinidad, at the time of the studies in the 1960's, there was a shortage of nesting sites in caves, and no feeding area was too far distant.

The massive post-breeding departure of an estimated 10,000 birds from the Caripe cave, leaving only a few hundred in the post-breeding months, may be a somewhat irregular occurrence. C. Bosque has suggested that such behaviour may be due to the loss of palms locally, as these should form one of the principal sources of food at that time of year. In other Venezuelan caves with breeding populations of over 1000 birds, however, the numbers roosting there in the post-breeding months falls to as low as only two birds. Similar behaviour has been suggested for caves in both Colombia and Ecuador, so post-breeding dispersal or nomadism may be of widespread occurrence in the Oilbird.

The home range of breeding Oilbirds has been estimated to be 85-95 km², with feeding localities as much as 150 km away. The remains of an Oilbird, thought possibly to have been an immature, and presumably killed by collision with a utility wire at

3100 m in Costa Rica, suggests that the species may be resident locally. However, the nearest known Oilbird cave is some 700 km away, by direct flight, in Colombia, as no Costa Rican or Panamanian Oilbird caves have been reported so far. The distance that Oilbirds disperse from known roosting caves remains mostly a matter of conjecture at the present time, and it is worth noting that one marked Oilbird in Venezuela flew 240 km in a single night to another cave.

Relationship with Man

In 1799 Humboldt and his companion, the botanist Amie Bonpland, were led by missionaries to the famous cave near the village of Caripe, Venezuela, to view the local ornithological sight: the impressive emergence at dusk of thousands of Oilbirds from this large cave. It was Humboldt who coined the name *Steatornis* from the Greek *stear* meaning "fat" or "tallow", and the English translation, Oilbird, has been used ever since. The village of Caripe is just six kilometres from the cave, and the source of the species name *caripensis*.

Far earlier, in 1678, a Capuchin monk, Fray Francisco de Tauste, described, in missionary documents, the dense clouds of birds that came out of the Caripe cave at night. He described the tasty oil that was made from squabs, and reported that the local Indians believed the souls of their dead went into this same cave. Oilbirds were then, and still are, called *Guácharos* in most of their native lands, a word said to come from archaic Spanish or possibly even Catalan meaning "crying, or making a loud lament". Throughout the species' range, fat nestling Oilbirds are, or have been, collected by indigenous inhabitants for their famous oil. The young are cooked to extract the oil which is reported to be odourless and clear, and to keep well. This oil is used mainly in cooking, but also in some places for lamp oil. There are reports of the use of adult and nestling Oilbirds for their meat, said to be palatable, even though the birds have a somewhat musky odour. Venezuelans have also used the stomach contents of Oilbirds in folk medicine.

Visitors to an Oilbird cave should take suitable precautions against histoplasmosis. This disease is caused by the airborne fungus *Histoplasma capsulatum* that, although widespread throughout the world, can cause in humans a reaction from mild to occasionally fatal, and can permanently damage the lungs or eyes of some individuals. The fungus, not known from the Oilbirds themselves, lives in highly nitrogen-enriched soils below large bird and bat roosts. When the dry soil is stirred by human activity or winds, the fungus is easily inhaled. Recent Oilbird researchers in Venezuela have all worn surgical masks at all times, as a precaution against this disease because the fungus is known to be especially widespread in Venezuelan caves; it is generally believed that wetter caves are less dangerous.

Status and Conservation

There are no figures on the world population of Oilbirds. The birds are easy enough to count at dusk when they are leaving small caves, but the large numbers that fly out together from such caves as Caripe, estimated by some researchers to be some 10,000 but by others only 5000, can not be counted accurately. Furthermore, counts are complicated by the recently discovered dispersal or nomadic behaviour of some South American populations.

Historically, suitable breeding and roosting caves have been the limiting resource for all Oilbird populations. Recent cave explorations in Venezuela have raised the total to as many as 54 caves used, or recently used, by Oilbirds. The discovery, in the mid-1980's, of several large Oilbird caves in the Venezuelan state of Bolívar on the border of Brazil may have doubled the estimated number of Oilbirds in Venezuela. In this mountainous *tepuí* area one cave, Aguapira, was reported to support as many as 10,000 Oilbirds. The combination of caves located in difficult forested terrain, and often on the poorly explored borders of South American countries, suggests that there may be more unknown populations of Oilbirds awaiting discovery.

While in most countries the Oilbird is protected by law, active nestling collecting was still being practised in Peru in the 1960's, and in Trinidad, Venezuela and Ecuador in the 1970's; in some remote areas it probably continues up to the present. Over time Oilbirds probably reacted by nesting on the highest and least accessible ledges and shelves in their caves. Even so, in Venezuela seven of 54 colonies, all in small caves, have been deserted, though this is apparently due to loss of foraging habitat close to large human populations; similarly, five of 13 caves in Trinidad have been abandoned by Oilbirds in recent years.

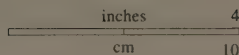
Humboldt recognized the problem of conservation when he learned of the massive raids on nestlings in the outer chambers of the Caripe cave. But he concluded that the annual harvest of thousands of nestlings was apparently sustainable due to reinforcements by birds breeding where the people could not reach the nestlings. There were, he said, Oilbird caves in the area with entrances too restricted for humans to enter, and also he heard Oilbirds in the Caripe cave far beyond the point where the native Indians refused to pass. In those days even the missionaries could not make the Indians go deep into the cave. The Indians believed the birds were ghosts of their ancestors, and to go far into the cave would be to enter the land of the dead. B. Snow, in her investigation of Oilbirds in the Los Tayos caves of Ecuador in 1976, again found human predation on nestlings, but she also believed that it too was sustainable because many of the nests were inaccessible.

In spite of the known and well-documented records of Oilbird predation by humans, it is the relentless attack on subtropical forests by the ever-increasing number of subsistence farmers in all range countries that pose the greatest long-term danger, as they threaten traditional Oilbird food resources. Tannenbaum and Wrege point out one fortuitous situation: many of the Lauraceae trees traditionally saved to shade coffee plantations are also those that are important in the Oilbird's diet. On the other hand, many of the palms that Oilbirds depend on during non-breeding months are selectively sought out and destroyed by man. An important *Euterpe* species is the source of the well-known edible Heart-of-palm, which is commercially canned and exported from Venezuela. Much of this product is gathered from palm trees in unregulated forests and the extraction of the heart kills the palm. Thus man's interests are in direct competition with the Oilbird's requirements. Few efforts are being made to cultivate the *Euterpe* palm for its heart, because it takes so long to grow to harvestable maturity.

Oilbirds, however, sow their own seeds. Roca's study of cast seeds in the Caripe cave suggested that most of the seeds covering the cave floor were regurgitated by nestlings. No seeds were found in collecting trays under nests that were being incubated, so adult birds were regurgitating the seeds, as many as 50 per bird per day, outside the cave before they returned. These he calculated to amount to about 21 t of seeds a month for this colony.

This fact formed the key to a major conservation action taken recently in Venezuela. Radio-telemetry had shown that through the year the birds of the Caripe cave spent much of their time foraging outside the protected area. Following the recommendations of Tannenbaum and Wrege, and also of Roca, the government in 1989 set aside an additional 66,400 ha area, the Mata de Mango, 15 km east of the already protected 15,500 ha Caripe cave area for the Oilbirds. Two other significant factors were involved: the Caripe cave and its Oilbirds are very well known throughout Venezuela, and a large tourist attraction; furthermore, by setting aside the new area as a National Park, it also protected the entire catchment area of the small Río San Juan which is currently important to both local agriculture and nearby commercial maritime petroleum transportation.

In Bolivia, Peru, Trinidad, and Colombia governments have set aside areas near and surrounding Oilbird caves, or are planning to do so. Protecting just the breeding or roosting caves will not succeed in saving the birds, because sizeable tracts of primary forest must also be included. In order for these plans to succeed, specific efforts will have to be made to overcome the usual problems of lack of money for personnel to enforce the national laws, and the lack of official will to oppose the small agricultural enterprises that constantly and permanently damage subtropical forests.



Family STEATORNITHIDAE (OILBIRD) SPECIES ACCOUNTS

PLATE 21

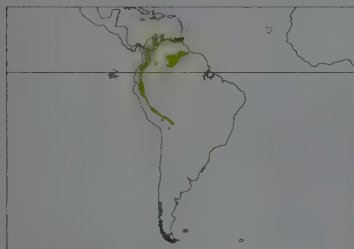
Genus *STEATORNIS* Humboldt, 1814

Oilbird

Steatornis caripensis

French: Guacharo des cavernes **German:** Fettschwalme **Spanish:** Guácharo
Other common names: Diablotin (Trinidad)

Taxonomy. *Steatornis caripensis* Humboldt, 1817, Caripe, Venezuela. Shows some owl-like features, but nowadays generally considered to be a caprimulgiform; regarded as an early offshoot within the order, probably closest to Nyctibiidae and Caprimulgidae. Monotypic.
Distribution. Panama and Colombia E to Venezuela, Trinidad, Guyana and N Brazil and S to Ecuador, Peru and Bolivia; also recorded in Costa Rica.



Descriptive notes. 40-49 cm; 350-485 g. Rich chestnut-brown all over with numerous white spots and diamonds edged with black; paler below with smaller white diamonds; large white spots on wings and outer rectrices; laterally compressed long hooked bill with stiff long vibrissae at triangular base; brown iris; long wings and a graduated tail held in inverted V; short, weak pink legs and toes. Fledglings as adults: no juvenile plumage. **VOICE.** Orientates within dark caves by means of echolocation clicks. Typical calls within caves are series of shrieks, screeches and screams; makes softer calls outside.

Habitat. Diurnal roosting and breeding takes place in caves and grottos, usually in mountainous areas of subtropical forests; locally occurs from sea-level up to over 3400 m. Forages in primary tropical and subtropical forests.

Food and Feeding. Feeds entirely on fruits: mainly of palms throughout the year, and aromatic Lauraceae, Burseraceae and others seasonally; fruit, 1-6 cm diameter, gathered only at night by small flocks hovering in flight and tearing whole fruits from high trees; only pericarp is used, with seed regurgitated undamaged; nestlings are fed on the same fruits. Nocturnal foraging distance up to 150 km.

Breeding. Attempt takes 4-5 months, starting at end of dry season: laying mainly Apr to early May (Mar-Jul) in Trinidad; mainly May-June in Venezuela. Monogamous, apparently on long-term ba-

sis. Nests colonially on shelves and ledges high up, usually in dark caves; nests are hard thick piles used in consecutive years, with a slight edged cup at top. Eggs 2-4 in Trinidad, 1-3 in Venezuela; rarely second nestings; both sexes co-operate in all nesting tasks; incubation 32-35 days; chicks hatch nearly naked, but are down-covered by 30 days; young are very slow-growing due to frugivorous diet; by day 70, nestlings are very fat and weigh 50% more than adults; loss of weight begins c. day 75 with concurrent growth of adult-like feathers; fledging near adult weight at c. 88-125 days; young generally do not return to natal cave, post-fledging care unknown. Age of sexual maturity unknown; one bird known to have lived over 12 years in the wild.

Movements. Post-breeding dispersal from continental South American caves; some nomadism particularly by juveniles. Other movements poorly known, but adults of Trinidad populations occupy same cave all year round. A group seen at Hillsborough Dam in 1988 was first record from Tobago, birds presumably having flown c. 30 km over sea from Trinidad.

Status and Conservation. Not globally threatened. Colonies have survived long history of predation by man of nestlings for fat in all range countries (see page 250). At present, most serious threat is loss of subtropical forests and their fruiting trees, to primitive slash-and-burn agriculture. No accurate figures of overall numbers available for whole of range. Easily the most accurate figures come from Venezuela, where 54 colonies have been located, and species is known from at least 19 more sites, but 7 of the colonies have been abandoned, seemingly due to loss of foraging habitat; main centres are in N Monagas (21 colonies, possibly supporting c. 20,000 birds) and S Bolívar (large colonies), followed by Falcón (c. 900-1400 birds) and Anzoátegui (500-800 birds), with smaller numbers elsewhere; largest colonies known are those at Aguapira (Bolívar) with c. 10,000 birds, followed by several in Monagas, notably Caripe (5000-10,000 birds), Cueva Grande (c. 5000 birds) and Cueva Clara (1000-2000 birds); total population of Venezuela may number c. 40,000-50,000 birds or rather more. Detailed information lacking for Colombia, but total numbers reckoned to be similar to or slightly lower than those for Venezuela; human disturbance judged to be more intensive in Colombian Andes. No information on status in S of range, where known colonies are widely scattered. In 1962, population of Trinidad estimated to number 1460 adult birds. Species not known to be kept in captivity.

Bibliography. Barrowclough *et al.* (1997), de Bellard (1957), Bosque (1978, 1986, 1988), Bosque & Parra (1992), Bosque & Ramírez (1988), Bosque *et al.* (1995), Brumfield *et al.* (1997), Cade & Temple (1995), Cannell (1986), Cherrie (1907), Chubb (1916), Chwind *et al.* (1997), Cleere (1998), Collins (1983), Fjeldså & Krabbe (1990), Garrod (1873), Griffin (1953, 1954), Gutiérrez (1991, 1994), Herklots (1961), Hilty & Brown (1986), Humboldt (1817, 1852), Ingram (1958), Johnston (1988), Konishi & Knudsen (1979), Korzoun (1991), Lambie (1993), Lentino (1990), Lindholm (1988), Meyer de Schauensee & Phelps (1978), Olson (1987), Ortiz (1979), Ortiz & Carrión (1991), Parker, T.A. *et al.* (1982), Parker, W.K. (1889), Pearman (1995), Pettigrew & Konishi (1984), Ramírez, J.E. (1954), Ramírez, R. (1987), Rasmussen *et al.* (1996), Remsen & T aylor (1989), Ridgely & Gwynne (1989), Roca (1991, 1994), Roca & Gutiérrez (1991), Ross (1965), Rutgers & Norris (1972), Sibley & Ahlquist (1972, 1990), Sick (1993), Snow, B.K. (1979), Snow, D.W. (1961, 1962b, 1976, 1985), Snow, D.W. & Snow (1978), Snyder (1966), Stiles (1988), Stolzenburg (1991), Stolzmann (1880), Stotz *et al.* (1996), Suthers & Hector (1985), Tannenbaum & Wrege (1978, 1979, 1984a, 1984b), Thomas *et al.* (1993), Voous (1983), Wetmore (1968a), White, S.C. (1974), Willard *et al.* (1991), Williams & Tobias (1994), Zimmer (1930).

Class AVES

Order CAPRIMULGIFORMES

Suborder CAPRIMULGI

Family AEGOTHELIDAE (OWLET-NIGHTJARS)



- Small to medium-sized nocturnal birds, with wide but rather weak bill, short legs and upright stance when perching.
- 18-30 cm.



- Australasia.
- Mainly forests or woodland, one species extending into open, dry scrubland.
- 1 genus, 9 species, 18 taxa.
- 1 species threatened; none extinct since 1600.

Systematics

Aegothelidae forms possibly the most distinctive subgroup within the Caprimulgiformes, and it is sometimes separated from the other families in its own suborder or superfamily. In the rather upright stance and the tendency towards a facial disc with eyes looking forwards, the owllet-nightjars show a certain similarity to owls (Strigiformes). A few anatomical characters shared by owls and owllet-nightjars, as well as the hole-nesting behaviour and unmarked white eggs common to both groups, suggest that these similarities may be at least partly due to affinity rather than to convergent evolution. Indeed, the DNA hybridization data obtained by C. G. Sibley and J. E. Ahlquist show the owls as the closest relatives of the Caprimulgiformes and the Aegothelidae as the most ancient surviving offshoot of the early caprimulgid stock, somewhat in conflict with the traditional view that the Oilbird (*Steatornis caripensis*) would occupy this position.

The two largest species, the Feline Owllet-nightjar (*Aegotheles insignis*) and the Moluccan Owllet-nightjar (*Aegotheles crinifrons*), were in the past sometimes separated from the other species in a separate genus, *Euaegotheles*, but this classification has been abandoned following the demonstration that supposed differences in their skeletal anatomy and in the size of the oil-gland do not really exist. All the living species are therefore now placed in the genus *Aegotheles*.

An extinct owllet-nightjar from New Zealand is known through numerous bones from deposits that extend up to the Holocene (the last 10,000 years). These were named as *Megaegotheles novaezealandiae*, the placement in a separate genus being based on the relatively long and strong legs shown by the fossils, which may have reflected more terrestrial activity than occurs in any of the living species of owllet-nightjar. It is now known, however, that the rare New Caledonian Owllet-nightjar (*Aegotheles savesi*) also has rather long legs, although these are less developed than in the New Zealand fossils, and this has resulted in the merging of the genus *Megaegotheles* into *Aegotheles*.

Another significant fossil of an owllet-nightjar is that named in 1977 as *Quipollornis koniberi* from the early to middle Miocene of eastern New South Wales, Australia. The single, partly associated skeleton differs from *Aegotheles* in proportions and in sufficient qualitative features as to leave little doubt of its generic distinctiveness. *Quipollornis* is valuable in showing that the Aegothelidae have a long history in the Australasian faunal region, which is the only region in which living

representatives of the family are known. Nevertheless, that discovery was eclipsed by the report in 1982 of a fossil aegothelid from the Phosphorites du Quercy in France, the deposits being older than those in New South Wales, and dating from the Upper Eocene to the Upper Oligocene. Along with a few finds of early Tertiary fossils of other caprimulgid families in the "wrong" continents, such as the spectacular records of frogmouths (Podargidae) and potoos (Nyctibiidae) in Europe, the Quercy aegothelid suggests that the early biogeographical history of the order was much more complicated than might be suggested by the ranges of its living taxa.

Several of the owllet-nightjar species are very poorly known and the genus appears rather uniform in most respects, so that it



As their English name implies, owllet-nightjars show characteristics somewhat intermediate between nightjars and owls. While the usual taxonomic treatment places them alongside the former, several anatomical features, along with their upright stance and hole-nesting habits, suggest an ancestral affinity with the latter. The legs and feet of the Australian Owllet-nightjar, in common with its congeners, are larger and stronger than in other Caprimulgiformes, perhaps as a result of a more terrestrial lifestyle.

[*Aegotheles cristatus*, Australia.
Photo: Len Robinson/FLPA]

The wings of owlet-nightjars are markedly rounded, an adaptation to their habitat and foraging behaviour. Although little is known about the feeding techniques employed by most species, the evidence suggests that they usually fly short distances in well-vegetated habitats, movements facilitated by paddle-shaped wings.

While this feature is conspicuous in the Australian Owlet-nightjar, its wings are in fact less rounded than those of its relatives while its tail is longer, presumably because it inhabits more open country. It also differs from most other members of the family in its less pronounced facial bristles, but resembles them in that its eyes are oriented forwards and set in facial discs.

[*Aegotheles cristatus*
cristatus,
near Keith,
South Australia.
Photo: Nicholas Birks/
Auscape]



is difficult to arrive at a sequence of species that reflects their evolutionary relationships. Despite these difficulties, two groups of species may be tentatively placed as the "least advanced" and the "most advanced" within the genus. The three large species, the Feline Owlet-nightjar, the Moluccan Owlet-nightjar and the Spangled Owlet-nightjar (*Aegotheles tatei*), show considerable superficial similarities to some Asian frogmouths (*Batrachostomus*), including a wide and rather strong bill; similar patterns of coloration, especially on the scapulars and underparts; predominantly rufous ground colour of plumage; parallel-edged and slightly pointed rectrices; and similar long semi-bristles over the ear-coverts. Hence, the size and other characters of those three species might be regarded as ancestral features in the genus, even though some of their similarities to frogmouths could be the result of convergent adaptations to similar lifestyles within rain-forest habitats.

The Australian Owlet-nightjar (*Aegotheles cristatus*) may be the most advanced species of the genus, with adaptations to life in open woodland habitat that include finely barred grey plumage; more pointed wings than in any congener; extensively frayed trailing edges to its remiges; a relatively long tail with broad feather tips; relatively large feet; black stripes on the crown; and somewhat shortened facial bristles. The Barred Owlet-nightjar (*Aegotheles bennettii*) shares many of the features of that species, while the New Caledonian Owlet-nightjar may be a more divergent member of the same group since it also has a predominantly barred pattern on its otherwise rather featureless dark plumage.

The remaining three species are tentatively placed between those least advanced and most advanced groups of species. Of the three, Wallace's Owlet-nightjar (*Aegotheles wallacii*) shows little evidence of close relationship to any congener, whereas Archbold's Owlet-nightjar (*Aegotheles archboldi*) and the Mountain Owlet-nightjar (*Aegotheles albertsi*) constitute an extremely similar pair of sibling species that apparently replace each other in different regions or mainly at different elevations in the mountains of New Guinea.

There are several uncertainties regarding the limits of species in this genus. Some of these difficulties arise because museum specimens are few, so that the problem of judging the taxonomic status of allopatric representatives, which is familiar in many other groups of birds, becomes harder to solve in the absence of specimens from zones of potential range contact. Moreover, lack of knowledge of the living birds, especially of their vocalizations, tends to increase the difficulties when attempting to make objective decisions about species limits in such cases as these.

Thus, with Wallace's Owlet-nightjar the well-marked subspecies *gigas* could well be treated as a distinct species, although another subspecies, *manni*, appears to be intermediate in some respects between *gigas* and the nominate form. A comparable problem exists in judging the status of the Vogelkop population, *affinis*, of the Barred Owlet-nightjar. It now seems clear that *affinis* does indeed belong with that species rather than with the Australian Owlet-nightjar, in which it was formerly placed by some authors, but it may be better regarded as a separate species; the absence of information on its voice makes it harder to decide the best treatment.

The very recent proposal to split the Spangled Owlet-nightjar as a distinct species from the Feline Owlet-nightjar is another instance of poorly known allopatric populations being of rather uncertain status, but in this case one form is montane and the other, the Spangled, is a lowland bird. Furthermore, recent studies by T. K. Pratt have demonstrated numerous hitherto unrecognized differences between the two in coloration and in details of structure, as well as providing additional specimens of the Spangled Owlet-nightjar, one of which extends its known range by over 1000 km eastwards from the type locality. The new information seems sufficient to tip the balance in favour of affording the Spangled Owlet-nightjar full species rank, although this treatment is not universally agreed upon.

Archbold's and the Mountain Owlet-nightjars present a different kind of problem in delimitation of species. They are so similar that some museum specimens cannot be confidently as-



One of the largest and most beautifully patterned members of the family, the Feline Owlet-nightjar, inhabits montane evergreen forests in New Guinea. This rufous morph individual shows the broad bill, open nostrils and conspicuous facial bristles characteristic of the family. While the function of these bristles is essentially unknown, they may help guide prey into the gape of foraging birds or serve as sensitive "whiskers" to help them navigate in dark nesting and roosting cavities. The widely spaced mandibles presumably assist in trapping mobile insect prey, either in flight or from surfaces such as trees or the ground. The difficulty of observing most owlet-nightjars is evinced by the fact that ecological data for this species, and several of its relatives, are almost entirely lacking. No nest or egg has ever been reported, and although its diet can be deduced from the gut contents of specimens, its foraging behaviour remains to be described.

[*Aegotheles insignis*,
Saruwaged Mountains,
Huon Peninsula,
Papua New Guinea.
Photo: W. Peckover/
VIREO]

signed to one or the other, a problem further aggravated by the wide variability in coloration of both of them. They are regarded as distinct species mainly because both have been collected at around 2062 m near the Wissel Lakes in Irian Jaya, where it seems that their altitudinal ranges meet, with Archbold's Owlet-nightjar occurring mainly at higher elevations and the Mountain Owlet-nightjar at lower elevations. Nevertheless, it remains a possibility that a single species exhibiting polymorphism in plumage coloration is really involved, with the different morphs mainly having different altitudinal ranges. Field studies in the Wissel Lakes region may shed light on this, especially if it can be demonstrated that the currently unknown voice of Archbold's differs from that of the Mountain Owlet-nightjar and thus serves as a species-isolating mechanism.

Variation between different populations within the Australian Owlet-nightjar is complex and unusual, resulting in a wide disparity in the numbers of subspecies recognized by different authors, with from two to eight forms bearing subspecies names in different accounts. This species' geographical variation in size is unusual in that the largest birds occur in the north of the range, in southern New Guinea, and the smallest in the south, with intermediates in the intervening area. This pattern is the opposite of that normally found, where the largest birds generally occur in colder regions, a phenomenon so widespread that it is known as Bergmann's Rule. Because the large New Guinea birds appear to be merely the end point of this clinal pattern of size variation, they are no longer afforded separate subspecific status. Variation in coloration of Australian Owlet-nightjar populations is also complicated, because in some regions the females occur as two colour morphs (with many intermediates), and there is much individual variability, too. As a rule, paler birds occur in the arid inland regions of northern and central Australia and darker birds in the more humid coastal districts of the south and east. Also, the rufous-morph females become more common in arid regions

of north-west Australia. Large series of specimens show, however, that much of this variation in coloration is clinal and intergrading, so the only subspecies now kept apart from the nominate form is the Tasmanian population, *tasmanicus*, which not only has dull, mainly sooty-grey plumage without any rufous tone but also has a disproportionately short tail.

Morphological Aspects

Structural features regarded as characteristics of the family include a wide but not especially strong bill; nostrils that are obvious and open, and placed near the tip of the bill; a desmognathous palate; the absence of basipterygoid processes; two carotid arteries; a sternum with two foramina (notches) on each side; no intestinal caeca (unlike all other Caprimulgiformes); pelvic muscle formula AXY; the absence of powder-down, but the presence of a large naked oil-gland; legs and feet larger and stronger than in most Caprimulgiformes; the number of phalanges in the outer toe not reduced; and the middle toe without pectination on its claw. Like the frogmouths, the owlet-nightjars have well-developed facial bristles, but as with that family their functions are largely unknown. It is tempting to suggest that the bristles may serve to direct prey into the gape during hunting, and perhaps act as tactile "whiskers" that help the birds in moving about and locating nestlings inside dark nest-holes, but detailed studies are needed to investigate such possibilities in a proper and methodical manner.

The wings of all owlet-nightjar species are more or less rounded, corresponding to feeding behaviour that mainly involves short sallying flights (see Food and Feeding). The Australian Owlet-nightjar has somewhat longer and more pointed wings than any of the other species and has a particularly long, full tail. This species commonly inhabits more open woodland than its conge-

The plumage of owlet-nightjars varies within species. Female Australian Owlet-nightjars, for example, are found in grey or rufous morphs, while males tend to be grey. Populations of arid regions are consistently paler or more rufous than those of moister regions, in apparent accordance with variations in soil colour. Adult plumage is coarsely barred with prominent pale facial markings while that of young birds, such as this one, is finely speckled and more uniform. In each case, patterns and colours effectively function as camouflage, helping the species to evade the attentions of predators.

[*Aegotheles cristatus*
cristatus,
Hattah-Kulkyne National
Park, western Victoria,
Australia.
Photo: Hans and
Judy Beste/Ardea]





The Mountain Owlet-nightjar usually frequents the understorey or middle storey of humid forest habitats in the New Guinea highlands. It has not been recorded below 800 m and ranges up to an impressive 3700 m, a truly montane distribution. It sometimes occurs at areas of forest edge, in gardens and in tree-fern savanna. Like other members of the family, it is generally secretive and nocturnal in habits, only seen by day when flushed from roosting sites. The bold white wing markings or modified remiges and rectrices so characteristic of many nightjars are absent in owlet-nightjars. The conclusion that intraspecific communication is conducted through vocal rather than visual signals is supported by the fact that no aggressive or courtship display has been recorded for any member of the family, except during nest defence.

[*Aegotheles albertisi albertisi*,
Arfak Mountains,
western New Guinea.
Photo: Richard Kirby/
BBC Natural History Unit]

ners, or even scrub in arid regions, so its structure may be related to feeding in more open situations.

The legs and feet are rather small and weak in most species of the genus, but slightly stronger in the Australian Owlet-nightjar than in most of the others. As already mentioned, the rare New Caledonian Owlet-nightjar has considerably longer, stronger legs and feet than the other species, while those of the extinct *Aegotheles novaezealandiae* of New Zealand were even better developed. Unfortunately, nothing is known of the lifestyle or former lifestyle of those two island endemics, although it has been inferred that they would be more active on the ground than other owlet-nightjars.

As with other families of the Caprimulgiformes, the coloration of owlet-nightjars consists of more or less sombre shades of brown, rufous, chestnut or grey, with or without a few bold markings of black or white. The two largest species, the Feline and the Moluccan Owlet-nightjars, have extensive areas of rufous to chestnut plumage, whereas the smaller species are mainly brown with a predominantly streaked pattern or grey to blackish with a predominantly barred pattern. In the Australian Owlet-nightjar, populations of the arid interior are commonly paler and more rufous than those of moister, better-wooded regions, whereas Tasmanian birds are very dark, each population apparently tending to match the prevailing colours of the soil. There can be little

doubt that the rather drab colours and the intricate patterns of streaking or barring exhibited by owlet-nightjars serve mainly to conceal them from predators. Where bolder signal markings are present they tend to be restricted to pale half-collars on the hindneck or bold patches on the scapulars, with none of the bold markings on the remiges or rectrices that characterize the true nightjars (Caprimulgidae). Very little information exists on the use of signal markings in communication by owlet-nightjars, but in any case it appears highly probable that much of their intraspecific signalling is by voice rather than by visual means.

Sexual dichromatism tends to be slight or absent, and the coloration of juveniles, where known, differs from that of adults mainly in having less well-defined markings, with pale half-collars and scapular spots weak or non-existent. Several species show well-marked variation in coloration, such that the extremes have been regarded as colour morphs, as for example in both sexes of the Feline, Archbold's and Mountain Owlet-nightjars and females of the Australian Owlet-nightjar. Confusingly, much of the literature on New Guinea birds refers to these morphs as "phases", a term which might more appropriately be reserved for age-dependent plumages. In any event, among these owlet-nightjars individuals showing intermediate coloration are common, so that it may be better to regard them as examples of very variable coloration rather than true polymorphism.

The Australian Owlet-nightjar often occurs in dry woodland dominated by Eucalyptus or Acacia trees. It is also found in many other environments including evergreen forest, mangroves, mallee scrub and shrubland, while some individuals even feed well away from trees in open grassland. In all habitats, this species occasionally perches at the entrance to roost- or nest-holes at twilight and occasionally in the middle of the day. While this behaviour might relate to birds warming themselves in sunlight, very little is known about its function. The birds usually only emerge if the roost tree is tapped or scraped, in response to which they normally fly directly into another roost-hole. Most territories have several available holes that may be used in rotation. The reluctance of the birds to perch in the open during daylight is unsurprising, given their vulnerability to predation and the fact that they are sometimes mobbed by passerine birds in mistake for owls.

[*Aegotheles cristatus*
cristatus,
Northern Territory,
Australia.

Photo: Jean-Paul Ferrero/
Auscape]



Habitat

Most owl-nightjars are essentially forest birds, although the Australian occurs mainly in more open habitats and the habitats of the New Caledonian are not reliably known.

Of the seven forest species, four are primarily lowland birds, with maximum recorded elevations of 1800 m for the Moluccan, 1540 m for Wallace's, 1125 m for the Barred and 100 m for the rare Spangled. In the case of the poorly known Wallace's Owllet-nightjar, however, different races may have different altitudinal ranges, since the nominate form is known at 0-1125 m whereas the race *manni* is recorded only at about 985-1110 m. Besides inhabiting the forest interiors, the Moluccan and Barred Owllet-nightjars have been reported from forest edge and the Moluccan occasionally also in lightly wooded areas of cultivation and in coconut plantations.

The remaining three forest species are essentially montane birds, with recorded altitudinal ranges of 1150-3000 m for the Feline, 2062-3600 m for Archbold's and 800-3700 m for the Mountain. The altitudinal ranges of the sibling pair of Archbold's and Mountain Owllet-nightjars may show little or sometimes no overlap in regions where they both occur, such as in the Wissel Lakes area where both were found at 2062 m; the Mountain is found mainly at lower altitudes, with Archbold's mainly higher up. Besides their forest strongholds, all three of these montane species extend into other habitats, the Feline into forest edge, second growth and riverine woodland, the Mountain into forest edge, gardens and tree-fern savanna, and Archbold's probably into subalpine scrub in the highest parts of its range.

The Australian Owllet-nightjar shows several adaptations to more open woodland habitats (see Systematics, Morphological Aspects). This species sometimes occurs inside evergreen forest, among tall mangroves or in open forests dominated by eucalyptus (*Eucalyptus*), but it more typically occurs in open woodlands or tall scrub such as mallee. It also inhabits a wide range of open, low shrublands and it sometimes feeds away from trees in open grassland.

General Habits

Owlet-nightjars are secretive nocturnal birds that are infrequently seen during the daylight hours, and then only when they are acci-

dentally disturbed from roosting sites. Several species are so poorly known that even their roosting sites have remained undescribed, but it is known that the Feline, Mountain and Barred Owllet-nightjars often roost in tree holes and that these are the usual sites for the comparatively well-known Australian Owllet-nightjar. Other roosting sites described for the Feline Owllet-nightjar are in clusters of dead leaves or tangled vines, and for the Mountain Owllet-nightjar in dark tangles of shrubbery or bamboo and the hollow end of a broken-off tree fern, while a Barred Owllet-nightjar was once reported roosting on a branch. Sites used less frequently than tree holes by the Australian Owllet-nightjar are other types of hole or crevice, including crevices in cliffs or banks, hollows in termite mounds and inside roofs of derelict homesteads or abandoned nests of *Pomatostomus* babblers. Roosting Australian Owllet-nightjars are reported to remain alert, crouching with head erect, breast on the floor of the hollow and feet tucked up under the body.

There are several observations of owl-nightjars awake at the entrances to their roosting holes during the day, as well as a few reports of the Australian Owllet-nightjar "sunning" itself at the hole entrance on cold winter days. Details of the choice of roosting sites are available only for this species, which is known to use sites 2-8 m and occasionally 11 m above the ground and holes varying from shallow to 2 m deep. The same sites may be used year after year, although some territories contain as many as six roosting holes that may be used in rotation. If the roosting tree is tapped or scraped, the bird usually flies out quickly, often moving directly into another hole; sometimes, however, the bird peers from the entrance hole before disappearing back inside, clambering down tail first. Since owl-nightjars which perch in the open during daylight are commonly mobbed by honeyeaters (*Meliphagidae*) as if they were owls, and because they may be at risk from predators, it is perhaps not surprising that they are unwilling to stay in the open for very long during daylight.

Almost all activity occurs between dusk and dawn. In the Australian Owllet-nightjar there appear to be peaks of activity in the evening and for an hour before dawn, with a lull in the middle of the night. This species often drinks after dusk and towards dawn, flying down to squat at the edge of a pool of water.

Information on the pattern of social organization is available only for the Australian Owllet-nightjar, and even that species is poorly known for such a widespread and common bird. Although often appearing to be solitary, it is believed to pair for life, with

Nothing has been published about the diet or feeding behaviour of the Barred Owllet-nightjar. The scant information available suggests that owl-nightjars may employ a broad spectrum of techniques to collect their insect food. Although they usually sally from perches and are capable of plucking prey from hard surfaces without landing, they have also been observed feeding aerially, and eating ants without flying at all. The discovery of earthworms in some stomachs provides further evidence that a certain amount of terrestrial foraging takes place.

[*Aegotheles bennettii* bennettii,
Goldie River,
Port Moresby,
Papua New Guinea.
Photo: Eric Lindgren/
Ardea]



Although the Australian Owlet-nightjar usually nests in trees, its nest-holes have also been recorded in fence posts, fallen logs, man-made structures and riverbanks. The clutch, usually of 3-4 eggs, is incubated for around 25 days. When disturbed at the nest, adults or well-developed young often sit tight and may hiss at intruders as a threat display, revealing a large pink gape, while puffing out their feathers to increase their apparent size. Recent studies show that breeding adults, eggs and young are very vulnerable to mammalian predators.

[Left: *Aegotheles cristatus cristatus*, mallee eucalypt forest, Hattah-Kulkyne National Park, Victoria. Photo: Tom and Pam Gardner/FLPA.

Right: *Aegotheles cristatus cristatus*, near Lake Broadwater, Darling Downs, southern Queensland. Photo: Cyril Webster]



the paired birds roosting in close proximity to each other throughout the year. The pairs are well spaced, apparently defending territories with areas of about 10-80 ha, although very few data are available. The churring call of this species presumably functions as territorial advertisement and defence, since the birds respond to playback of recordings by calling and sometimes by approaching. There is, however, almost no information on threat displays or other behaviour likely to be involved in defence of territories.

Knowledge of the comfort behaviour of the members of this family is extremely scant, although the Australian Owlet-nightjar is known sometimes to preen inside its roosting hollow and to head-scratch indirectly. Aggressive and courtship displays have not been described for most of the species, and much of their intraspecific communication is likely to be through vocalizations rather than posturing.

Voice

Vocalizations of the Spangled, Archbold's and New Caledonian Owlet-nightjars are undescribed and apparently unknown, and there are very few accounts of those of the Feline Owlet-nightjar. The reputation that several of these species have for being elusive and rare may well be lessened once their voices are described, as locating them will then be easier.

Only the Australian Owlet-nightjar can be regarded as well known vocally and it is remarkable that this species apparently has only four main types of call, far fewer than those species of frogmouth (*Podargus*) or typical nightjar (*Caprimulgus*) for which the vocabulary has been well described. By far the commonest call of Australian Owlet-nightjars is a rather high-pitched, grating, rattling "chirr-chiirrr", of two or three units. It is given throughout the year, by both sexes, normally from a perch, although calling in flight has been reported. There can be little doubt that the churring has the function of territorial advertisement, so that it could be referred to as "song". Louder, sharper and more abrupt versions of the churring call are sometimes ut-

tered by day from the roosting hole. The other vocalizations reported for the species are given only in special contexts: a high-pitched "yuk" by an adult calling fledging young from the nest; hissing by brooding birds giving threat display towards an intruder; and a low trilling by young begging for food, and perhaps also by adults when feeding young.

The call of the Barred Owlet-nightjar is described as a deep trill or a descending hollow "churr", which is apparently reminiscent of the commonest call of the Australian Owlet-nightjar, of which this species is regarded as a close relative. The Mountain Owlet-nightjar, however, has an entirely different call, described as three (sometimes two or four) downslurred whistles, each higher-pitched than the preceding one; an account of its giving an unpleasant-sounding, slowly delivered "whor whor-whor" may represent no more than another rendering of the same call.

The calls of the Moluccan Owlet-nightjar have recently been described for the first time and these, too, appear to be quite different from those of any congener. This species utters a wide variety of manic screams and cackles and responds to imitations of these. The most frequent call, apparently used in territorial advertisement, is a moderately weak, upslurred squeal or scream immediately followed by three short, unhurried screams on the same pitch. Others of the species may respond to that call with louder or more hurried versions of it. The alarm call is described as a series of wild, maniacal, blood-curdling screams and a cat-like yowling call.

Food and Feeding

The diets of the Spangled, Wallace's, Archbold's and Barred Owlet-nightjars are entirely unknown. For two more species the data on diet are very few, based on the unique type of the New Caledonian Owlet-nightjar having beetle remains in its stomach and on the gut contents of Feline Owlet-nightjars being recorded as insects, including beetles. Nothing has been reported of the feeding techniques for any of those species.



After being found in a felled tree, these Australian Owlet-nightjar chicks were hand-raised and successfully released. The darker plumage of the Tasmanian race *tasmanicus* is apparently already visible. In normal circumstances, nestlings acquire juvenile plumage after about 20 days and fledge around a week later. There is some evidence that they then continue to accompany their parents for several months, but further study is required to verify this.

[*Aegotheles cristatus tasmanicus*, Tasmania.
Photo: Roland Seitre/Bios]

Rather little is known of the food and feeding of two other owlet-nightjar species. The Moluccan Owlet-nightjar takes small insects by sallying from perches in the middle storey of the forest, catching them in flight or by hover-gleaning from leaves. Studies using stomach-flushing of captured birds and faecal analyses show that Mountain Owlet-nightjars feed mainly on insects, mostly Coleoptera but with some Lepidoptera, Diptera and Orthoptera, but that they also take a few earthworms. Although this species forages at night beneath the forest canopy, its feeding techniques are unknown, so that the presence of earthworms in the diet provides useful evidence that some of its food is caught on the ground.

Information on diet and feeding techniques is more complete for the Australian Owlet-nightjar. This species feeds mainly by sallying from perches, capturing insects in its bill. Typically, it swoops onto prey from a low perch, taking insects from the ground or tree trunks, often without landing. It sometimes also picks up food, such as ants, while standing on the ground, or sallies upwards from the ground to take insects in flight. Occasionally, when insect prey is plentiful, it may feed mainly on the wing, making flights with rapid, regular wingbeats for up to about 30 m, mainly low over the ground. The diet recorded from gut contents of Australian Owlet-nightjars includes a wide variety of small insects and also spiders and millipedes. Most records are of beetles (Coleoptera), grasshoppers and their allies (Orthoptera) and ants (Hymenoptera), but other orders of insects recorded include Hemiptera, Dictyoptera (Blattodea), Lepidoptera (caterpillars and imagines) and Dermaptera. A record of seeds and vegetable debris in one stomach can presumably be attributed to the plant materials being ingested accidentally. Details of hunting behaviour and prey selection await accurate study, although it seems clear that prey are located and tracked visually and that individual insects are pursued.

Breeding

As with other aspects of the biology of owlet-nightjars, lack of information makes it difficult to generalize about their breeding.

Nests of six of the species, the Feline, Spangled, Moluccan, Wallace's, Archbold's and New Caledonian Owlet-nightjars, have not been described and are apparently unknown, while all that has been reported on the nesting of the Barred Owlet-nightjar are the measurements of its eggs and the fact that they are white and lack markings. Sparse information on the breeding seasons of several of these species has been derived from the sizes of gonads of collected specimens and the occasional record of a fledgling, but patterns remain unclear.

Two nests of the Mountain Owlet-nightjar have been described, both in hollows in dead tree stubs. In each case the nest contained a single white egg, but these may have been incomplete clutches.

The Australian Owlet-nightjar is the only member of the family for which breeding has been studied in detail. This species nests in holes, usually in trees, but occasionally in fence posts, fallen logs, crevices in derelict buildings or burrows in riverbanks. Nest-holes are generally 1-5 m above the ground, but occasionally at ground level or up to 20 m up, or, rarely, much higher. The nest, with an entrance 7-25 cm in diameter, is placed 0.3-3.5 m down inside the hollow, but in most cases no deeper than 1 m. Both sexes usually share in building a mound of fresh leaves or pieces of bark, on which the eggs are laid. The frequent use of fresh leaves of *Eucalyptus* or *Acacia* possibly suggests some benefit from insecticidal or insect-repellent properties of these leaves.

Laying occurs from August to December throughout the wide Australian range of the species. A report that it "may breed in any month, especially following rain in dry and arid regions" appears to be incorrect. Furthermore, and contrary to some reports, it appears that only a single brood is reared each year, although replacement clutches may be laid, sometimes in the same nest, if the first clutch is lost. The eggs are slightly glossy, rounded-oval to elliptical in shape, and have unusually thick shells. They are normally white; references to occasional clutches being marked with light spots or with pale brown presumably refer to soiled eggs. To date, eggs are known only for three species, the Mountain, Barred and Australian, and all fall within the range 27-32 x 21-25 mm. Clutches are usually of three or four eggs, rarely two or five, and eggs are laid at intervals of one or two

days. Incubation is carried out by the female, and perhaps also by the male, for a period of 25-27 days.

Hatching is spread over several days, confirming that effective incubation starts when the first egg is laid. The nestlings hatch covered in a white first down and are brooded day and night until their eyes open on the fourth or fifth day, and thereafter only by day until the grey second down emerges on about the 11th or 12th day. Only one adult normally broods, the other usually roosting by day in a tree-hollow nearby. If a brooding adult is disturbed at the nest, it generally sits tight and gives a threat display with the plumage puffed out, gaping to show the pink mouth, and hissing. The adults cease brooding entirely after about the 11th day, roosting close to the nest but not in the same hollow. Both parents then share in hunting for food and feeding the young, the feeding visits often lasting only for several seconds. As no nest sanitation is carried out after about the 11th day, droppings accumulate in the nest. Nestlings are fully feathered by about 14-17 days, but they remain in the nest for at least another seven days. During that period the adults hunt right through the night, feeding the young every 10-15 minutes throughout the first half of the night. Nestlings beg for food using a low trilling call, and adults are reported sometimes to respond with the same trilling sound when they are feeding their young. The nestling period is 21-29 days, rarely 32 days, although 35 days has been recorded in captivity.

The chicks fledge abruptly in the middle of the night, still with strands of down attached to their body plumage. Thereafter they apparently never return to the nest. It has been reported that juveniles remain with their parents for several months after fledging, but the duration and nature of post-fledging care need further study.

Movements

All species of Aegothelidae are believed to be sedentary, although some as yet undocumented dispersal of juvenile birds presumably occurs. The presence of Australian Owlet-nightjar populations on coastal islands such as Bathurst, Melville, Fraser and Kangaroo, as well as on Tasmania and in New Guinea, may suggest that some wandering or some dispersive movements have

at times been made by this species, but its populations are normally regarded as sedentary, whether in the arid Australian interior or in cold-winter regions of Tasmania and South Australia.

No instance of extralimital vagrancy has been reported for any member of this family, but the occurrence or former occurrence of taxa in the Moluccas, New Caledonia and New Zealand must presumably have resulted from past vagrancy, albeit perhaps at times when these landmasses were closer to Australia or New Guinea.

Relationship with Man

As retiring nocturnal birds that live mainly at low densities in forests, it is hardly surprising that owlet-nightjars infrequently come to man's notice, and even local tribespeople know little about them. Nevertheless, the Australian Owlet-nightjar became known to early European settlers under names that included Little Nightjar and Fairy, Little or Moth Owl.

Even the early ornithologists appear to have been less excited by their discovery than might be expected. The generic name *Aegotheles* given to these birds was merely a Greek version of "goatsucker", doubtless borrowed from its Latin equivalent of *Caprimulgus*, which was the familiar name for nightjars. For the modern ornithologist they remain one of the most challenging groups of birds: the Australian Owlet-nightjar must vie with few others for being the most poorly known bird that is common throughout Australia, while the nests, calls and behaviour of several of the Papuan species remain totally unknown. Modern techniques such as voice-recording and the use of playback to capture birds in mist-nets, radio-tracking and light-tagging, and the use of night-vision devices will surely allow a much fuller knowledge of them to be gained in the future.

Status and Conservation

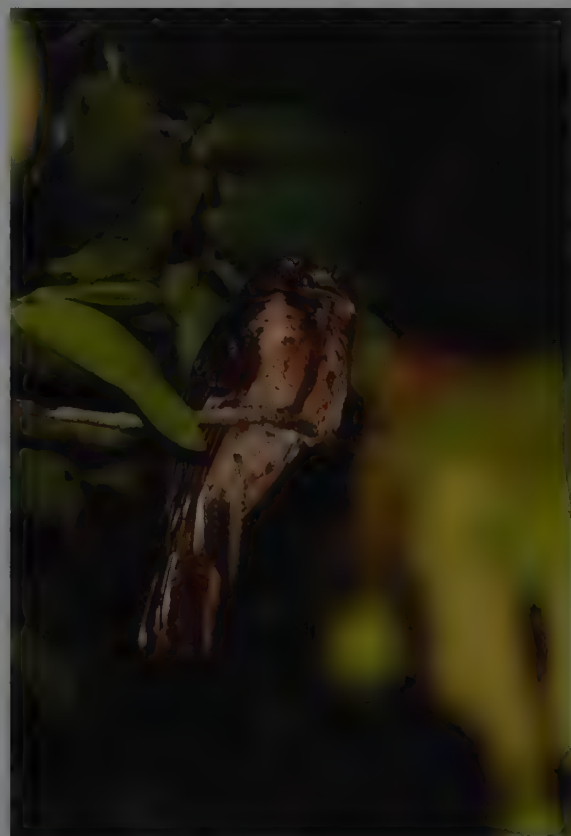
Although known only from skeletal remains, the endemic owlet-nightjar of New Zealand, *Aegotheles novaezealandiae*, became extinct during the Holocene, and there is some circumstantial evidence that it survived until after the arrival of early Polynesians (Maoris) in New Zealand, only some 1000-800 years ago. Hence, its extinction may well be attributable directly or, more likely, indirectly to man's actions. The New Caledonian Owlet-nightjar was reliably known only from fossils and from the skin of a specimen collected in 1880, until the very exciting sighting of a single bird by J. Tobias and J. K. Ekstrom in November 1998. Contrary to the widespread trend for avian extinctions occurring on islands, the Moluccan Owlet-nightjar was recently reported to be common on Halmahera.

The lowland and montane forests of New Guinea support more species and subspecies of owlet-nightjar than any other region, and some of these are known only from a few specimens. Nevertheless, large areas in New Guinea have hardly been explored ornithologically and much forest remains, despite the encroachment of logging activity in some regions. It is likely therefore that improved ornithological knowledge, and particularly knowledge of owlet-nightjar calls, will reveal further populations of the scarcer forms.

The Australian Owlet-nightjar still remains one of the commonest and most widespread of nocturnal birds in Australia, although it is only sparsely distributed in Tasmania. This species' tolerance of varied types of woodland and scrub, even small patches in farmland regions, suggests that it is not currently at any great risk of decline, despite many road casualties and rather numerous losses due to introduced predators.

General Bibliography

Bock (1994), Brumfield *et al.* (1997), Burrell (1914), Cannell (1986), Cleere (1998), Glenny (1955), Hartert (1892, 1897), Mariaux & Braun (1996), McEvey (1985), Olson *et al.* (1987), Peters (1940a), Pratt & Pratt (1998), Rich & Scarlett (1977), Rose (1976), Scarlett (1968), Schönwetter (1964), Serventy (1985b), Sibley & Ahlquist (1990), Sibley & Monroe (1990), Sibley *et al.* (1988), Stettenheim (1974), Strahan (1994).



The Moluccan Owlet-nightjar is found at forest edge on Halmahera. Until recently, it was very poorly known, but recent reports have suggested it to be surprisingly common, occurring in at least one reserve and one proposed protected area. Its toleration of degraded habitats suggests that for the time being it may be reasonably secure. Although several members of the family are almost unknown in life, it is hoped that increased survey work within their ranges and improved knowledge of their vocalizations will result in further positive revisions of status.

[*Aegotheles crinifrons*, near Batu Putih, near Sidangoli, Halmahera, Moluccas. Photo: Frank Lambert]

PLATE 22

inches 4
cm 10

brown morph

rufous morph

brown morph

1

2

3

rufous morph

rufous morph

5

brown morph

brown morph

6

rufous morph

intermediate morph

4

7

ssp bennettii

8

ssp terborghi

9

♂

♀

rufous morph



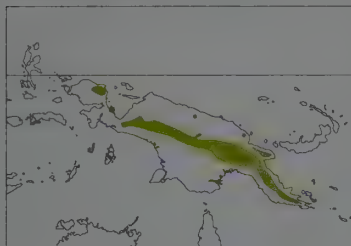
Genus *AEGOTHELES* Vigors & Horsfield, 1826

1. Feline Owlet-nightjar

Aegotheles insignis

French: Grand Égothèle **German:** Käuzchenschwalm **Spanish:** Egotelo Grande
Other common names: Large/Reddish/Rufous Owlet-nightjar, Rufous Owlet-frogmouth

Taxonomy. *Aegotheles insignis* Salvadori, 1875, Hatam, Arfak Mountains, New Guinea. Perhaps forms superspecies with *A. crinifrons* and *A. tatei*; latter until recently treated as conspecific with present species, but studies suggest that it should be afforded specific rank (see page 253). Birds of SE New Guinea formerly separated in race *pulcher*. Monotypic.
Distribution. Mountains from Vogelkop to SE New Guinea.



Descriptive notes. 28-30 cm; 59-85 g. Probably the largest of the owlet-nightjars. Mainly brown or dark rufous, upperparts with few whitish spots or streaks and prominent lateral crown-stripes; throat white or buff, breast and belly boldly spotted whitish. Well-defined brown morph and rufous morph, connected by intermediates. Little information on juvenile; one described as being of rufous morph. **VOICE.** Little known, although rising series of slightly trilled "owrr" notes and single or repeated squeaky "kee" notes reported; a "foh... foh" call also described.

Habitat. Montane forest, especially primary forest and edges, but also reported from second growth and from riverine woodland in otherwise open country. Mainly 1150-2800 m, occasionally up to 3000 m.

Food and Feeding. Gut contents show that diet consists of insects, including beetles. Feeding behaviour has not been described.

Breeding. Season little known; birds in breeding condition collected Apr, May, Aug and Sept and a fledgling in Nov. Nest-site presumed to be a tree-hollow, but nest and eggs undescribed.

Movements. Presumed to be essentially sedentary.

Status and Conservation. Not globally threatened. Widespread and, where much forest habitat remains in the mountains of New Guinea, species can be at least locally frequent, e.g. frequently recorded in Tari Valley.

Bibliography. Andrew (1992), Beehler (1978), Beehler *et al.* (1986), Coates (1985), Coles (1995), Diamond, J.M. (1972, 1985), Eastwood (1989b), Gilliard & LeCroy (1961), Gregory (1995a, 1995b), Majnep & Bulmer (1977), Mayr (1941a), Mayr & Gilliard (1954), Mayr & Rand (1937), Peckover & Filewood (1976), Rand (1941, 1942b), Rand & Gilliard (1967), Ripley (1964a), Rowland (1995b), Sims (1956), Stresemann & Stresemann (1966).

2. Spangled Owlet-nightjar

Aegotheles tatei

French: Égothèle de Tate **German:** Tiefland-Käuzchenschwalm **Spanish:** Egotelo de Rand
Other common names: Rand's Owlet-nightjar

Taxonomy. *Aegotheles insignis tatei* Rand, 1941, low elevations at headwaters of Fly River, New Guinea.

Possibly forms a superspecies with *A. insignis* and *A. crinifrons*. Formerly treated as lowland race of *A. insignis*, but recent studies indicate that it is a separate species (see page 253). Monotypic.

Distribution. EC New Guinea at headwaters of R Fly and Amazon Bay.



Descriptive notes. c. 25 cm. Rather similar to montane *A. insignis*, but differs in notably smaller size, considerable reduction of white markings, especially on underparts and above eyes, and rufous-brown rather than blackish-brown underwing; tail pattern also differs; several other differences are rather less obvious. Juvenile plumage unknown. **VOICE.** Not described.

Habitat. Lowland forest.

Food and Feeding. No information.

Breeding. No information.

Movements. No information; presumed to be sedentary.

Status and Conservation. Not globally threatened. Known from only 4 specimens taken at 2 localities, so it is either a rare species or much overlooked. Extensive lowland forests remain in the regions from which it has been recorded, so the species is unlikely to be under any immediate threat.

Bibliography. Beehler *et al.* (1986), Coates (1985), Diamond, J.M. (1985), Pratt (1999), Pratt & Pratt (1998), Rand (1941), Rand & Gilliard (1967).

3. Moluccan Owlet-nightjar

Aegotheles crinifrons

French: Égothèle des Moluques **German:** Molukkenschwalm **Spanish:** Egotelo Moluqueo
Other common names: Halmahera/Long-whiskered/Painted Owlet-nightjar

Taxonomy. *Batrachostomus crinifrons* Bonaparte, 1850, no locality = Halmahera. Possibly forms a superspecies with *A. insignis* and *A. tatei*. Monotypic.

Distribution. Halmahera, Kasiruta and Bacan in N Moluccas.



Descriptive notes. c. 29 cm. Large owlet-nightjar. Upperparts finely vermiculated greyish-brown; underparts paler, variably spotted dark. Apparently has brown morph and rufous morph with intermediates, as in *A. insignis*; rufous morph less patterned, and more rufous above and on breast. Juvenile plumage unknown. **VOICE.** Recently described for first time. Wide variety of manic screams and cackles. Most frequent call, apparently used as territorial song, is a moderately weak, upslurred squal or scream immediately followed by 3 short unhurried screams on same pitch; other birds may respond with louder or more hurried versions. Alarm described as a series of wild, maniacal, blood-curdling screams and a cat-like yowling call.

Habitat. Lowland and hill forests; also tall secondary forests, forest edge and occasionally lightly wooded cultivation and coconut plantations. Recorded from sea-level up to 1800 m.

Food and Feeding. Small insects. Feeds by sallying for small aerial insects from perches in middle storey; also by hover-gleaning from leaves.

Breeding. No information available.

Movements. Presumably sedentary, but scanty information available.

Status and Conservation. Not globally threatened. Restricted-range species: present in Northern Maluku EBA. Known from few specimens. Little information, although species was found in 1994 on the site of the proposed Halmahera National Park, and was recently described as common on this island. Also known to occur at Mt Sibela, Bacan.

Bibliography. Andrew (1992), Bonham (1995), Coates & Bishop (1997), Lambert (1994), Lambert & Yong (1989), Olson *et al.* (1987), Stattersfield *et al.* (1998), Sujatnika *et al.* (1995), White & Bruce (1986).

4. Wallace's Owlet-nightjar

Aegotheles wallacii

French: Égothèle de Wallace **German:** Fleckenschwalm **Spanish:** Egotelo de Wallace
Other common names: White-spotted Owlet-nightjar

Taxonomy. *Aegotheles wallacii* G. R. Gray, 1859, Manokwari, New Guinea.

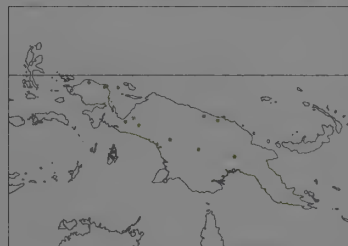
Probably not closely related to any congener. Race *gigas* has been proposed as a distinct species on basis of its considerably larger size and its montane rather than predominantly lowland range, but this treatment countered by the fact that *manni* is of intermediate size and occupies an intermediate altitudinal range; recent studies show that the three races differ significantly only in size. Three subspecies recognized.

Subspecies and Distribution.

A. w. wallacii G. R. Gray, 1859 - New Guinea in Vogelkop and along S side of Central Ranges E to Karimui; Aru Is.

A. w. gigas Rothschild, 1931 - Weyland Mts (W New Guinea).

A. w. manni Diamond, 1969 - N Coastal Range of New Guinea (Mt Menawa, Mt Turu).



Descriptive notes. 20-23 cm; 46.5-48.5 g (*wallacii*), 50.5-52 g (*manni*). Distinctive small owlet-nightjar. Nominate form is variable in plumage, but apparently without showing any well-defined polymorphism and with sexes generally similar. Dark brown above, with pale speckles and vermiculations; buffy-white to greyish-white below with dark spots or bars, breast mottled dark brown. Single apparent juvenile has crown all blackish-brown, marked only with fine irregular barring and speckling of buff, and heavily barred underparts. Races differ in size and sometimes in coloration; some *gigas* and *manni* have suggestion of white collar on hindneck. **VOICE.** Little information. Double whistle, first note rising, second falling and often with trill, may function as song; second note sometimes omitted.

Habitat. Forests, mainly hill and lower montane forests; occasionally enters gardens. Occurs from sea-level to 1540 m, but altitudinal range apparently varies with race; approximate range of nominate 0-1125 m, of *gigas* 1200-1540 m, of *manni* 985-1110 m.

Food and Feeding. Beetles reported. No other information.

Breeding. No reliable information available; published accounts of cream-coloured eggs with grey markings most unlikely to be based on those of an owlet-nightjar.

Movements. Presumably sedentary, but information scanty.

Status and Conservation. Not globally threatened. Apparently a rare, or perhaps elusive, species throughout its range, but unlikely to be immediately threatened since extensive forests remain within the ranges of all three of its subspecies.

Bibliography. Andrew (1992), Beehler & Finch (1985), Beehler *et al.* (1986), Coates (1985), Diamond (1969, 1972), Gregory (1995a, 1995b), Hartert *et al.* (1936), Mayr (1941a), Mayr & Meyer de Schauensee (1939b), Mayr & Rand (1936), Murray (1988), Olson *et al.* (1987), Pratt & Pratt (1998), Rand & Gilliard (1967), Rothschild (1931), Stein (1936).

5. Archbold's Owlet-nightjar

Aegotheles archboldi

French: Égothèle d'Archbold **German:** Archboldbergschwalm **Spanish:** Egotelo de Archbold
Other common names: Eastern Mountain Owlet-nightjar

Taxonomy. *Aegotheles albertisi archboldi* Rand, 1941, 2800 m altitude, 9 km north-east of Lake Habbema, New Guinea.

Formerly treated as a race of *A. albertisi*, but is apparently a sibling species, replacing it at higher elevations (see page 253). Monotypic.

Distribution. C New Guinea: known only from Wissel Lakes area, Nassau Range, N slope of Mt Wilhelm and Victor Emanuel Mts.



Descriptive notes. 18-20 cm; 29-35 g. Extremely similar to *A. albertisi*, from which even some well-made skins appear inseparable when series are compared under ideal conditions in a museum. Differs mainly in richer coloration of upperparts, with coarser dark barring and coarser white spots, and in underparts averaging darker, more richly coloured and more heavily marked; identification further complicated as both species have a rufous morph and a brown morph, connected by intermediates. Juvenile undescribed. Voice. Not described.

Habitat. Occupies montane forests, with reliable records at 2062-3600 m; reports from lower elevations may result from specimens being carried down from higher ground by native collectors. Probably lives in subalpine thickets at the upper limit of its range.

Food and Feeding. Unknown.

Breeding. No information.

Movements. Presumed to be sedentary, but information scanty.

Status and Conservation. Not globally threatened. Restricted-range species: present in Central Papuan EBA. Although species is known only from four small regions, it was apparently plentiful in some of them during the period from 1940's to 1960's, and extensive montane forests still remain there. Hence, the species is unlikely to be threatened, at least in the immediate future.

Bibliography. Andrew (1992), Beehler & Finch (1985), Beehler *et al.* (1986), Coates (1985), Diamond (1972), Gilliard & LeCroy (1961), Gregory (1995a, 1995b), Junge (1953), Mayr (1941a), Rand (1941, 1942b), Rand & Gilliard (1967), Ripley (1964a), Stattersfield *et al.* (1998), Sujatnika *et al.* (1995).

6. Mountain Owlet-nightjar

Aegothales albertisi

French: Égothèle montagnard

German: Bergschwalm

Spanish: Egotelo Montano

Taxonomy. *Aegothales albertisi* P. L. Slater, 1874, Hatam, Arfak Mountains, New Guinea.

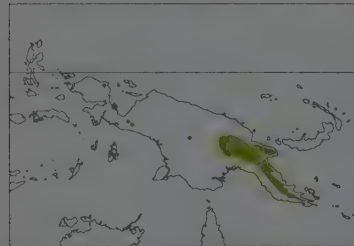
Apparently a sibling species of *A. archboldi*, replacing it at lower elevations (see page 253). Three subspecies recognized.

Subspecies and Distribution.

A. a. albertisi P. L. Slater, 1874 - Arfak Mts of Vogelkop in NW New Guinea.

A. a. wondiwoi Mayr & Rand, 1936 - Mt Wondiwai in Wandammen Peninsula.

A. a. salvadorii Hartert, 1892 - locally from Weyland Mts to SE New Guinea.



Descriptive notes. 18-20 cm; 36-40 g. Variable, and can be virtually indistinguishable from *A. archboldi*. Likewise, has a rufous morph and a brown morph connected by intermediates; a "grey phase" sometimes mentioned in the literature refers to brown morph, which is not really greyish. Single juvenile skin, apparently of present species, is mainly dull rufous above, with some obscure dark barring, and lighter beneath with many streaks of dull buff and inconspicuous spots of blackish-brown. Race *salvadorii* generally duller in coloration, with fewer and smaller markings on upperparts and less distinct banding on

outer rectrices; race *wondiwoi* larger than the other two. Voice. Call consists of 3 mournful whistles, each of them downslurred or at constant pitch. Series of squeaky "kee-kee" notes also described.

Habitat. Mostly forests on mountains, extending to forest edges, gardens and tree-fern savanna.

Altitudinal range reported as 800-3700 m, although in the relatively well-known E Highlands it occurs at c. 1385-2615 m.

Food and Feeding. Gut contents of specimens and other data show that diet consists mainly of insects (mostly Coleoptera, also Lepidoptera, Diptera and Orthoptera) but also includes a few earthworms. Reported to forage for insects at night beneath the canopy and in clearings of montane forests, but details of feeding technique undescribed.

Breeding. Few data on season; birds in breeding condition in Jun and Sept, eggs in Aug and Nov, and a nestling in Apr or May. Only 2 nests have been described, in hollow dead tree stubs, once at forest edge and once in primary forest, the former c. 3-5 m above the ground. Each contained a single white egg. Incubation and fledging periods and shares of sexes in care of eggs and young unknown.

Movements. Apparently sedentary.

Status and Conservation. Not globally threatened. Race *salvadorii* is apparently common in at least parts of its range. The small numbers of specimens known for the other two subspecies may reflect the paucity of ornithological studies within their ranges rather than real rarity. Extensive montane forests still remain over much of this species' historical range, and no immediate threats are evident.

Bibliography. Andrew (1992), Beehler (1978), Beehler & Finch (1985), Beehler *et al.* (1986), Coates (1985), Coles (1995), Diamond, J.M. (1972, 1985), Junge (1953), Mayr (1941a), Mayr & Gilliard (1954), Mayr & Rand (1936, 1937), Olson *et al.* (1987), Rand (1941), Rand & Gilliard (1967), Ripley (1964a), Schulz (1988).

7. New Caledonian Owlet-nightjar

Aegothales savesi

French: Égothèle calédonien

Spanish: Egotelo de Nueva Caledonia

German: Schwarzückenschwalm

Taxonomy. *Aegothales savesi* E. L. and E. L. C. Layard, 1881, Tongué, near Nouméa, New Caledonia.

Affinities difficult to judge, but plumage pattern and broad tail feathers are at least suggestive that present species may be most closely related to *A. bennettii* and *A. cristatus*. Possibly intermediate between extinct *A. novaezealandiae* (see page 252) and other members of family. Monotypic.

Distribution. SW New Caledonia.



Descriptive notes. 28 cm. A rather nondescript, dark-plumaged species known from a single specimen, an adult male. Entire plumage, including wings and tail, brown with narrow greyish-white barring. Several published illustrations purporting to represent this species are based on *A. cristatus* and are therefore considerably inaccurate. Voice. Not described.

Habitat. Recent record of bird in humid riverine forest at altitude of c. 1000 m; this individual was judged to be foraging in subcanopy. Otherwise habitat apparently unknown; various comments in the literature are only speculation.

Food and Feeding. Label of type specimen states "Food Coleoptera", doubtless on the basis of its gut contents. Recent record of bird thought to be foraging: the bird flew about, disappearing intermittently, at which times it was presumed to be perching.

Breeding. No information.

Movements. No information, but presumed to be sedentary.

Status and Conservation. ENDANGERED. Restricted-range species: present in New Caledonia EBA. Until very recently, no definite records since 1880, when the only specimen was collected, and species was thought possibly extinct, although the paucity of ornithological work in New Caledonia still allowed hope that it might survive. A report of one being killed during 1960's by a hunter in the Païta region, not far from the type locality, has remained unconfirmed. However, in Nov 1998 a single bird was seen in the Ni-Kouakou Reserve, S New Caledonia; despite subsequent searches during 4-month study, no further sightings, suggesting species is probably rare.

Bibliography. Collar *et al.* (1994), Delacour (1966), Hannecart (1988), Hannecart & Létocart (1983), Layard & Layard (1881), Mathews (1927), Mayr (1945), Olson *et al.* (1987), Stattersfield *et al.* (1998), Wagstaffe (1978).

8. Barred Owlet-nightjar

Aegothales bennettii

French: Égothèle de Bennett

German: Bennettschwalm

Spanish: Egotelo Barrado

Other common names: Bennett's/Collared Owlet-nightjar

Taxonomy. *Aegothales bennettii* Salvadori and D'Albertis, 1875, Hall Sound, south-east New Guinea. Regarded as conspecific with *A. cristatus* until the latter was discovered to occur in New Guinea within the range of present species, but the two are evidently close relatives. Race *affinis* has sometimes been suggested to be a race of *A. cristatus*, but its uniformly sooty coloration and rounded wings leave little doubt that it belongs instead with present species; nevertheless, recent studies suggest it may actually be better treated as a separate species. Five subspecies recognized.

Subspecies and Distribution.

A. b. affinis Salvadori, 1875 - Arfak Mts in Vogelkop Peninsula (NW New Guinea).

A. b. wiedenfeldi Laubmann, 1914 - N New Guinea from R Idenburg to Holnicote Bay.

A. b. terborghi Diamond, 1967 - Karimui Basin in E Highlands of Papua New Guinea.

A. b. bennettii Salvadori & D'Albertis, 1875 - S coast of SE New Guinea from R Koembe E to Milne Bay.

A. b. plumiferus E. P. Ramsay, 1883 - Fergusson I and Goodenough I (D'Entrecasteaux Archipelago).



Descriptive notes. 20-23 cm; 45-47 g. Sexes apparently similar, and there appears to be no polymorphic variation. Upperparts dark brown to blackish with narrow greyish-white vermiculations; broad pale buff eyebrows and whitish to buff hindneck-collar; underparts pale greyish to whitish-buff with broad spots and bars. A juvenile specimen has only a vague indication of the pale half-collar on hindneck. Races differ in both coloration and size; *terborghi* (known from a single specimen) apparently the most distinctive, being considerably larger than other forms and with darker, blackish upperparts. Voice. Call has been described as a deep trill or a descending, hollow "churr".

Habitat. Mainly lowland forests and their edges, normally up to c. 1000 m elevation, although the unique type of *terborghi* was collected at c. 1125 m.

Food and Feeding. No information available.

Breeding. Very little information. A recently fledged juvenile collected in Oct. Eggs are unmarked white, but nest-sites and clutch sizes seemingly not recorded.

Movements. Apparently sedentary.

Status and Conservation. Not globally threatened. Nominate race appears to be not uncommon, but there is very little recent information on the status of the other subspecies. Nevertheless, considerable areas of rain forest still exist in most regions of New Guinea, so none of the forms seems likely to be threatened.

Bibliography. Andrew (1992), Beehler (1978), Beehler & Finch (1985), Beehler *et al.* (1986), Coates (1985), Diamond (1967, 1972), Mathews (1927), Mayr (1937b, 1941a), Mayr & Rand (1935, 1936, 1937), Mees (1982b), Pratt & Pratt (1998), Rand (1942b), Rand & Gilliard (1967), Schodde & Mason (1981), Schönwetter (1964), Stresemann & Stresemann (1966).

9. Australian Owlet-nightjar

Aegothales cristatus

French: Égothèle d'Australie

German: Baumschwalm

Spanish: Egotelo Australiano

Other common names: Crested/Savanna Owlet-nightjar

Taxonomy. *Caprimulgus cristatus* Shaw *et al.*, 1790, New South Wales = Sydney area.

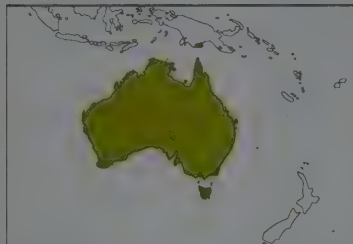
Apparently a close relative of *A. bennettii*, and formerly considered conspecific; *A. bennettii affinis* sometimes erroneously included within present species. Variation complex, but much of it clinal.

with largest birds in N of range; population in S New Guinea formerly treated as separate race, *major*, but appears to represent no more than end-point of size cline of nominate form; several other races listed in old literature are based on individual or polymorphic variation in coloration. Two subspecies currently recognized.

Subspecies and Distribution.

A. c. cristatus (Shaw *et al.*, 1790) - SE New Guinea between R Oriomo and Tarara (Port Moresby region); Australia.

A. c. tasmanicus Mathews, 1918 - Tasmania.



Descriptive notes. 21-25 cm; 35-65 g. Dark grey on upperparts, with pale spots and thin vermiculations; distinct pale eyebrows, rear crown-band and hindneck-collar; paler, often buff-coloured on underparts, with narrow brown vermiculations. Sexes frequently similar but female varies between a grey morph and a rufous morph, latter being particularly well marked in parts of N Australia, although intermediate birds are very common in some regions; extreme rufous morph apparently does not occur in male, although some males can be found with intermediate coloration. Juvenile resembles adult, but has slightly softer and sometimes more finely speckled plumage, shorter tail, somewhat shorter facial bristles, and pattern of black and whitish markings on crown and nape blurred or lacking. Race *tasmanicus* small, with disproportionately short tail, and upperparts rather uniformly dark sooty-grey. **VOICE.** Much the commonest call is a rather high-pitched, grating, rattling "chirr-chiirrr" of 2 or 3 units that doubtless serves to advertise territory. When disturbed, brooding adults may hiss while giving threat display.

Habitat. Open woodland, trees along watercourses, shrublands of *Eucalyptus* and *Acacia*, occurring especially in sclerophyll forests, tropical woodland and mallee; favours drier, more open, mature woodland and such taller shrublands as mallee; only occasionally recorded in tall mangroves, open grassland and rainforests. Sea-level to 1000 m.

Food and Feeding. Diet consists mainly of wide variety of small insects, with records of Dictyoptera (Blattodea), Coleoptera, Dermaptera, Hemiptera, Hymenoptera, Lepidoptera and Orthoptera; other invertebrates recorded are spiders and millipedes. Seeds and vegetable debris in the gut of a specimen may have been ingested accidentally. Feeds mainly by sallying from a perch to take insects and

other prey from the ground, from tree trunks or on the wing; when standing on ground, also picks up prey (e.g. ants) directly or flies up from ground to catch insects in flight.

Breeding. Season apparently the same throughout Australia, with eggs laid mostly Aug-Dec. Single-brooded; reports of second or third broods unconfirmed, although replacement clutches may follow loss of first. Sometimes makes no nest, but both sexes normally share in building mound of fresh leaves or pieces of bark; nests placed usually 1-5 m (0-20 m) above ground at bottom or end of vertical to horizontal hollow in tree or stump, rarely in fence post, fallen log, hole in building or burrow in riverbank. Clutch generally 3-4 eggs (2-5), white and unmarked, laid at intervals of 1-2 days; incubation by female, perhaps also by male, for 25-27 days; chicks hatch with dense, long and white first down, replaced after 7-10 days by long and grey second down, this in turn replaced by juvenile plumage a week or so before fledging; both parents brood and feed young, brooding continuously for first 4-5 days, then less constantly, all brooding and nest sanitation ceasing on c. 11th day; fledging 21-29 days (21-32); extent of post-fledging care needs confirmation, although it has been suggested that juveniles remain with their parents for several months after fledging.

Movements. Apparently sedentary throughout its range.

Status and Conservation. Not globally threatened. Widespread in Australia and moderately common over much of its range; sparser in Tasmania, where absent from some regions. Potentially at risk from competition for nest-holes with introduced Common Starlings (*Sturnus vulgaris*) in SE Australia and Tasmania, but there is no evidence of population decline. Recent study over five months in New South Wales has shown species to be rather vulnerable to mammalian predators, especially when it is nesting; of 7 radio-tagged adults, 4 were predated and 2 others disappeared in manner suggesting predation; of 6 nests studied, 4 failed to due to predation of adults, eggs or nestlings. Also suffers some mortality from domestic cats, from roadkills and perhaps from predation by goannas (*Varanus*). Nevertheless, the species seems able to withstand these pressures and to maintain its populations in settled regions.

Bibliography. Barker & Vestjens (1989), Bechler & Finch (1985), Beruldsen (1980), Blakers *et al.* (1984), Brigham & Geiser (1997), Brigham, Debus & Geiser (1998), Brigham, Gutsell *et al.* (1999), Brigham, Tremont *et al.* (1997), Burrell (1914), Cayley (1959), Coates (1985), Condon (1975), Debus (1996b), Diamond (1967), Dickison (1933), Draffan (1976), Fleay (1979), Frith & Frith (1993), Garnett (1993), Hall (1974), Higgins (1999), Hollands (1991), Kutt (1994), Lindsey (1992), Macdonald (1988), Mayr (1941a), Mayr & Rand (1935, 1937), McAllan & Bruce (1989), Mees (1961), Muller & Clayton (1972), North (1909), O'Brien (1990), Olson *et al.* (1987), Pizzey & Doyle (1998), Quested & McBride (1996), Rand & Gilliard (1967), Rose (1973a, 1974, 1976, 1997a), Rutgers & Norris (1972), Schodde & Mason (1981), Schodde & Tiedemann (1986), Schönwetter (1964), Serventy & Whittell (1962, 1976), Simpson & Day (1998), Strahan (1994), Stresemann & Stresemann (1966), Tronson & Tronson (1987), Wahlberg (1990), Webb (1989).

Class AVES

Order CAPRIMULGIFORMES

Suborder CAPRIMULGI

Family PODARGIDAE (FROGMOUTHS)



- Small to large, stocky nocturnal birds with strong, wide bill, short legs, and upright stance when perched.
- 19-60 cm.



- Oriental and Australasian Regions.
- Mainly forest or woodland, several species extending into second growth, wooded savanna or dry scrub; mostly at low elevations, some species reaching 2250 m.
- 2 genera, 12 species, 25 taxa.
- No species threatened; none extinct since 1600.

Systematics

The allocation of the frogmouths (Podargidae) to the order Caprimulgiformes has been accepted by virtually all recent systematists, but the details of their evolutionary relationship to the other families in the order are much less certain. The taxonomic ranking of subdivisions within the frogmouths is perhaps even more controversial, while the sequence of species in the two constituent genera poses problems that have often been ignored for lack of reliable information.

The DNA-DNA hybridization data of C. G. Sibley and J. E. Ahlquist serve broadly to support the deduction from anatomical and other characters that the frogmouths are an early offshoot of caprimulgiform stock, well separated from the owls (Strigiformes), less remote from the true nightjars (Caprimulgidae) than are the owl-nightjars (Aegothelidae), but somewhat more remote from them than are the potoos (Nyctibiidae).

The two living genera of Podargidae are known only in the Australasian Region, where the genus *Podargus* is found, and in the Oriental or Indo-Malayan Region, home of the genus *Batrachostomus*. Great excitement has been generated, therefore, by the discovery in recent decades of fossil Podargidae in the early Tertiary of Europe. The fossils are from Eocene strata at Messel in Germany, and (*Quercypodargus olsoni*) from the Upper Eocene Phosphorites du Quercy in France. These fossil records confirm the impression of the antiquity of frogmouths that one gains from the anatomical and DNA data, but the fossils themselves are too fragmentary to shed much light on evolution within the frogmouths.

Until the DNA-DNA hybridization data were published, it was thought that the two extant genera were clearly distinct from each other, although still rather obviously members of the same family since they share a similar general appearance, as well as many structural characters and life-history traits. The DNA results, however, suggested that *Podargus* and *Batrachostomus* diverged long ago, leading Sibley and his collaborators to advocate recognition of a separate family, the Batrachostomidae, for the Asian frogmouths. Some avian taxonomists would nevertheless argue that, for the purposes of determining what the taxonomic ranking should be, the considerable similarities between the two genera should outweigh information on the timing of their divergence. Since such an approach is deemed rather subjective, however, it does not find favour with modern systematists.

Differences between the two genera in external structure and anatomy are not great, although some clear differences do appear to show through (see Morphological Aspects). Furthermore, the nests of the two genera are distinctly different (see Breeding). It may therefore be that the divergence of *Podargus* and *Batrachostomus* was more ancient than their external appearances and life histories would at first suggest, so that we should indeed separate them at a higher taxonomic rank than that of genus. While it is probably better, for the time being, to maintain the traditional arrangement within a single family, further biochemical, anatomical, life-history or paleontological studies may indeed produce overwhelming evidence that two families are really needed. Thus, in this climate of uncertainty, the best option at present may be a middle course, that of recognizing two subfamilies, Podarginae and Batrachostominae. This compromise has



Subdivision of the
Podargidae

[Figure: Tim Worfolk]



Structural differences between the two frogmouth genera are rather slight. Members of *Batrachostomus* are mostly fairly small, while all three *Podargus* are large, the Papuan Frogmouth being the largest of all. Also, in *Podargus* the bill is somewhat larger and broader, and the facial bristles generally less developed, while the tail appears rather more pointed, mainly due to the overshooting pointed central pair of rectrices. Plumage tends to be paler and more marbled, no doubt reflecting the somewhat different habitat preferences of the two genera.

[*Podargus papuensis*, Iron Range, Cape York Peninsula, Queensland, Australia.

Photo: Clifford and Dawn Frith]



In addition to their slight morphological differences, Oriental *Batrachostomus* and Australasian *Podargus* are clearly separated on distribution. Also, their nests are quite distinct, being much smaller and slighter in *Batrachostomus*, like this Philippine Frogmouth. Recent DNA results show that the two genera probably diverged longer ago than originally thought, leading some taxonomists even to advocate their placement in separate families. However, on present evidence it may be more appropriate to split them off in two subfamilies, emphasizing their notable divergence, but also their common ancestry.

[*Batrachostomus septimus*, Raja Sikatuna National Park, Bohol, Philippines. Photo: Bill Simpson]

the advantage of maintaining the unity of the two groups, while highlighting their divergence.

Among the Australasian *Podargus*, the Marbled Frogmouth (*Podargus ocellatus*) shows some resemblance to *Batrachostomus* in coloration. On the basis of these similarities, its rainforest habitats and its wide distribution, it has been suggested that this species retains more ancestral characters than the other two *Podargus*

species. On the other hand, the Tawny Frogmouth (*Podargus strigoides*) may be the most "advanced" species of its genus, being adapted to relatively open and dry, *Eucalyptus*-dominated woodland habitats in Australia, where it captures much of its food by swooping to the ground. Its predominantly grey coloration, rather long and pointed wings, short tail and strong feet have all been interpreted as adaptations to these dry woodland habitats. Thus, the Marbled Frogmouth is now listed first in the sequence of species in the genus and the Tawny Frogmouth last, contrary to the arrangement in the older literature.

In his classic review of *Batrachostomus*, published in 1937, E. Stresemann listed the species roughly in order of decreasing size, although he gave no reason for doing so. Nevertheless, this may approximate to an evolutionary sequence, since phylogenetic analysis suggests that ancestral *Batrachostomus* may have resembled *Podargus* in being large and in showing little or no sexual dichromatism. If this is correct, the Large Frogmouth (*Batrachostomus auritus*) and the Dulit Frogmouth (*Batrachostomus harterti*) may have changed least from the ancestral type, whereas small species with strong sexual dichromatism, such as Horsfield's Frogmouth (*Batrachostomus javensis*), have undergone the most significant evolutionary change.

Morphological Aspects

Among the structural characters that have been used to define the Podargidae, the very wide, strong bill is the most obvious feature and is the one which gives the birds their common English name. In its bulk and shape it is quite distinct from the rather weak bill with wide gape that characterizes most Caprimulgiformes. Associated with the shape and strength of the bill are a desmognathous palate, and nostrils forming narrow slits near the base of the bill, each of them protected by a membrane and hidden by feathers and bristles. The wide, strong bill enables frogmouths to cope with tough, hard-shelled prey (see Food and Feeding), but it is attached to a surprisingly flimsy skull, such that torchlight shining into the open mouth of a living bird renders the surrounds of the eyes and other parts of the skull partly translucent.

Deeper anatomical characters include absence of basiptyergoid processes, palatines that are broad throughout, 13 cervical



vertebrae, a sternum with two pairs of posterior notches, and the presence of a single carotid artery, the left one. The wings are rounded, with the fifth, sixth or seventh primary the longest. The legs are very short, the tarsus being shorter than the middle toe, and both legs and feet are rather weak. Unlike the case of the Caprimulgidae, the number of bones, or phalanges, in the outer toe is not reduced, and the claw on the middle toe is not pectinated as it is in the true nightjars. Large patches of powder-down feathers are present on each side of the rump. The older literature stated that the frogmouth family lacks an oil-gland, but it has been established that this is true only of *Podargus* and that an oil-gland is present in *Batrachostomus*. The tongue of *Podargus* has a long, translucent, paper-like tip and was described as "certainly one of the most curious found in the Class of Birds", but the tongue of *Batrachostomus* has apparently not been described in detail. The arrangement of feathers (pterylosis) of *Podargus* has also been described as showing important peculiarities, but again there are no comparative details on feather-tract characteristics of *Batrachostomus*.

Structural differences between the Australasian *Podargus* and the Oriental *Batrachostomus* are not great, although members of the former are for the most part larger than those of the latter, the exception being that some Large Frogmouths overlap in size with the smallest individuals of *Podargus*, while the small species of *Batrachostomus* have no parallel in *Podargus*. Also, as already noted, an oil-gland is present in *Batrachostomus* but not in *Podargus*. A further difference between the two genera is that the central rectrices of *Podargus* are clearly longer than the next pair and have pointed tips, whereas *Batrachostomus* has the central pair only slightly longer than the others, with rounded tips. The extraordinarily wide bill is proportionately longer in *Podargus* than it is in *Batrachostomus*.

Facial bristles are well developed in all *Batrachostomus* species, but less so in *Podargus*. The "auricular plumes" of *Batrachostomus* consist of slender semi-bristles that are black or dark-coloured and long, often extending over the ear-coverts. However, the development of bristles on the front of the face and of auricular plumes varies somewhat among species, and even among subspecies in the Philippine Frogmouth (*Batrachostomus septimus*). As examples, the Sri Lanka Frogmouth (*Batrachostomus moniliger*) has relatively short facial bristles, whereas in

the Short-tailed Frogmouth (*Batrachostomus poliolophus*) they are particularly well developed, reaching lengths of up to 2.5 cm on the forehead and about 4 cm over the ear-coverts in the subspecies *mixtus*. The function of these bristles and semi-bristles is virtually unknown, and may vary according to their position on the head. It is tempting to regard long rictal bristles as helping to direct prey into the mouth and perhaps serving a tactile function, whereas auricular plumes may assist in shedding rain water.

The short legs of frogmouths reflect their arboreal habits and a lifestyle in which walking is usually restricted to a few shuffling steps along a branch, or, in some species at least, along the ground after they swoop down onto insect prey. In *Batrachostomus* the tarsi are partly feathered, but sex differences that have been reported in the extent of feathering apparently do not really exist. The postures of frogmouths when perching are typically more upright than those of nightjars, and the freezing, concealment postures sometimes adopted by most, if not all, species are often still more erect. The rounded wings correspond to feeding behaviour based on short sallying flights to pick prey from the ground, trunks or foliage, and at least two species even break off twigs for use as nest material while in flight. The wings are most conspicuously rounded in those *Batrachostomus* species that spend much of their lives in such dense vegetation as bamboo thickets or the dense understorey of lowland rainforest. The Tawny Frogmouth typically occurs in much more open habitats and hunts over open spaces, so it is not surprising that it has proportionately longer and more pointed wings, which presumably confer more rapid flight but with some loss of manoeuvrability. The flight of this species, however, is described as noiseless, like that of several other frogmouths.

As is normal among the Caprimulgiformes, the plumage coloration is mainly of rather sombre shades of chestnut, rufous, brown or greyish, although many species have beautifully intricate patterning. These drab tones are doubtless related to an overriding need for the birds to be concealed from predators, especially during the day, when they are roosting, but perhaps also at night, when owls may pose a threat. Any brighter signal markings usually consist of white spots or patches, occurring on the upper mantle as a half-collar, on the wing-coverts or on the scapulars, but these are of limited extent and are entirely absent in some species and absent from the juvenile plumages of others. The difficulties inherent in observing and studying nocturnal birds such as these probably account for the lack of published information on the usage of these signal markings, but many of the species may in any case rely more on vocalizations than on visual cues for communication.

At first sight, the colour and pattern of the plumage appear rather different in the two genera. Heavily streaked and elaborately vermiculated greys and browns predominate in *Podargus*, whereas many *Batrachostomus* species appear more uniformly rufous, although some, especially males, are heavily streaked. The pattern and coloration of *Podargus* may be related to the fact that two of the three species occur in relatively open habitats with many grey-barked trees, whereas most *Batrachostomus* are birds of dark, wet forest. The third *Podargus*, the Marbled Frogmouth, is a bird of lowland rainforest, and it shows the greatest similarities in coloration to *Batrachostomus*. This is especially true of females of the race *inexpectatus*, from the Solomon Islands: their plumage coloration is remarkably reminiscent of that of the Large Frogmouth of South-east Asia, although lacking the white hindneck-collar of the latter.

It is noteworthy that, where sexual dichromatism occurs, in both genera, the females tend to have slightly to considerably more rufous, or browner, coloration and less marked patterns of light and dark colouring. This is presumably related to the fact that, so far as is known for both genera, it is the males rather than the females that incubate during the day, suggesting that the need for cryptic plumage for predator avoidance is greater in males than in females.

Collectors preparing skins often make mistakes in determining the sex of bird specimens. This, together with the tendency for the females of some *Batrachostomus* species to look brighter than their males, has led to a number of errors or muddles in the literature over which sex has which type of plumage. With sev-

Horsfield's Frogmouth is shrouded in a good deal of taxonomic confusion. It has at times been considered conspecific with either or both of the Sunda (Batrachostomus cornutus) and Hodgson's Frogmouths (B. hodgsoni), and its two northern races have often been treated as forming a separate species, Blyth's Frogmouth (B. affinis). Even at the subspecific level there are problems: in central peninsular Thailand, where northern continentalis meets southern affinis, an intermediate population can be found. Birds on Palawan, too, are sometimes treated as a distinct race or even species.

[*Batrachostomus javensis*, Khao Noi Chuchi Non-hunting Area, southern Thailand.
Photo: Pete Morris]

Once located in the field, frequently no mean feat, a frogmouth can usually be easily identified as such, though it can be quite a challenge to determine the correct species or sex.

Frogmouths are restricted to the Oriental and Australasian Regions, whereas the potoos, to which they bear a superficial resemblance, are Neotropical birds.

All frogmouths are characterized by a big head and a massive, very slightly hooked bill of extraordinary width, strong enough to allow them to capture and swallow larger, tougher prey than nightjars. Both genera sport tufts of facial bristles, which spring mainly from the forehead but also from the ear-coverts. Despite various tentative suggestions as to their utility, their true functions remain a puzzle.

By means of subtle natural colours and much streaking and mottling the soft plumage of frogmouths affords great protection from danger as they are able to "melt" into their surroundings.

The species are variously patterned often according to the type of tree they roost in: the white blotching on the wing-coverts of this Tawny Frogmouth imitates to perfection the flaky nature of the tree bark and the lichens. When danger threatens, or the bird feels itself to be observed, it will adopt a "freezing" alarm posture by assuming a more upright stance, raising the bill and head skywards, and closing the eyes to mere slits, while a stump-like immobility completes the camouflage.

[*Podargus strigoides phalaenoides*, Cape York Peninsula, northern Queensland.
Photo: Clifford and Dawn Frith]





Frogmouths are highly sedentary birds, and have rather rounded wings, a short tail and weak legs and feet. Nevertheless, they can in fact fly strongly. Hunting at night from a branch, a bird will swoop down with silent flight on bowed wings to seize prey in its wide gape. The feet are not adapted for pouncing, and are used mainly for perching, though a bird may walk along a branch or, more briefly, on the ground, in search of food. The Tawny Frogmouth has longer and more pointed wings than most other frogmouths, reflecting its use of more open areas.

[*Podargus strigoides strigoides*, Lamington National Park, south-east Queensland. Photo: Glen Threlfo/Auscape]

eral of the species, matters have been complicated even further, because both sexes show polymorphic variation in coloration. For those species for which plenty of specimens are available, it now seems reasonably sure that the plumage types of each sex are properly understood, as for example with Gould's Frogmouth (*Batrachostomus stellatus*); but for others, such as the scarcer races of the Philippine Frogmouth, there are still doubts. Evidence of this may be offered by the recent describing of a new species of frogmouth, "*Batrachostomus pygmaeus*", from Busuanga Island, Palawan, in the Philippines. There seems to be a good chance that the single specimen upon which the description was based may actually have been an extreme or aberrant example of the race *affinis* of Hodgson's Frogmouth (*Batrachostomus hodgsoni*), which is resident on Palawan. Correctly sexed juvenile specimens are so few in collections that there is much uncertainty about the juvenile plumage of each sex for several of the *Batrachostomus* species.

Some statements in the literature rather confusingly refer to colour morphs as "phases", but the latter term is perhaps better avoided in this context, as more precisely referring to age-dependent plumages. When plumage variation due to subspecies, sex and age is taken into account, three species are found to show well-marked polymorphism in coloration: Gould's Frogmouth has chestnut-morph and dark-morph adults, apparently without intermediates; the Philippine Frogmouth has a chestnut morph, a mottled morph and intermediate individuals; and males of the Sunda Frogmouth (*Batrachostomus cornutus*) have a black-and-white morph and a brown-and-buff morph, along with intermediates. Despite the presence of intermediate birds, it seems better to describe the colour forms of these last two species as morphs, because they are very distinct visually.

Habitat

Most species of frogmouth are forest birds, but one has become wholly adapted to more open habitats with trees, and some of the characteristic forest species extend into other types of woodland.

The restriction to forest habitats is especially strong in the nine species of the genus *Batrachostomus*, with evergreen primary forest being the typical habitat of all but one of them. The

exception is the Sunda Frogmouth, which occurs mainly in second-growth forest and at forest edge, sometimes in plantations. Of the other eight species, however, the Large, Gould's, the Sri Lanka and perhaps also Horsfield's Frogmouths have been reported to occur sometimes in second growth, while the first of these also lives in swamp-forest, and the Sri Lanka Frogmouth extends into varied evergreen woodland and bamboo thickets. Perhaps the most remarkable extension of habitat preferences is



Over the years there has been a great deal of confusion in relation to frogmouth plumages, further complicated by the marked individual variation in colouring in most species and also by the presence of different colour morphs in some. Sexual dimorphism is quite noticeable in some taxa. Posing conveniently on the same branch to facilitate comparison, this pair of Marbled Frogmouths of the rare race *plumiferus* can be sexed by plumage differences: the female shows a plainer pattern and buffier coloration over all her underparts.

[*Podargus ocellatus plumiferus*, Gwongorella National Park, south-east Queensland. Photo: Marco Sacchi]

A little-known species, the Large Frogmouth is indeed the largest of its genus, overlapping in size with some of the smallest Podargus. It has a wide distribution in South-east Asia, though it is everywhere uncommon. Like all but one of its congeners, it is a true rainforest bird, frequenting the interior of primary lowland evergreen forests, though sometimes occurring in tall secondary growth, especially where a wealth of dense tangled vegetation offers plenty of cover in the middle and upper storeys.

[*Batrachostomus auritus*,
Gunung Palung National
Park, West Kalimantan,
Borneo.
Photo: Tim Laman]



shown by Horsfield's Frogmouth in Thailand, where the species occurs locally in mixed deciduous forest, including that on limestone crags. Unfortunately, it is not yet known whether or not it moves out of these deciduous habitats when the trees become bare of leaves.

The genus *Batrachostomus* includes lowland species and others of sub-montane areas. Among those inhabiting lowland forest are Gould's and Horsfield's Frogmouths, the former found only up to 500 m and the latter typically to 1600 m. The three sub-montane species are Hodgson's, Dulit and Short-tailed Frogmouths, the last of which occurs at 600-2540 m. One, the Philippine Frogmouth, has a wide altitudinal range, being found from sea-level up to 2500 m. Separation of some of the species of this genus at different altitudes might have resulted from competitive interactions, whereas the very wide altitudinal range of the Philippine Frogmouth may reflect the absence of congeners on the islands it inhabits.

Such ecological isolation in *Batrachostomus* through altitude, and also through habitat and body size, seems particularly clear in Borneo, which is the richest region for the genus, harbouring a total of six species. Two of them, one large and the other rather small, are sub-montane, and the other four are lowland birds. Of those four, the Sunda Frogmouth prefers second growth while the other three prefer primary rainforest; the three range in size from the Large Frogmouth, at about 206 g, to the tiny subspecies *affinis* of Horsfield's Frogmouth, weighing about 46.7 g, so size differences may prevent much competition among them. The considerable disparity between some of the species in relative length of the tail may be related to differences in hunting behaviour, and hence also serve to reduce interspecific competition.

In Australia, the three species of *Podargus* appear to be for the most part separated by their habitat preferences. The Marbled Frogmouth lives mainly inside evergreen forest, while the Papuan Frogmouth (*Podargus papuensis*) is found along forest edges; the Tawny Frogmouth inhabits a variety of drier types of woodland, many of them dominated by *Eucalyptus* species, as well as occurring in some types of scrub and in groves of trees in more open country. The large size of the Papuan Frogmouth may also serve to reduce competition where it meets the other two species.

The Tawny Frogmouth is absent or, at best, extremely rare and local in New Guinea, and there is some evidence that the

Papuan Frogmouth extends into more open habitats there, including groves of trees in savanna, than it does in Australia, providing a possible example of "adaptive release". Similarly, in the case of the Marbled Frogmouth, the smaller size of the races *ocellatus* in New Guinea and *plumiferus* in north Australia, which are sympatric with large-bodied congeners, compared with those that are not sympatric with congeners, namely *intermedius* in the Trobriand and D'Entrecasteaux Islands, *meeki* on Tagula Island (Louisiade Archipelago) and *inexpectatus* in the Solomons, may be indicative of "character divergence" related to presence or absence of interspecific competition.

All three *Podargus* species show a good degree of habitat tolerance. The Marbled Frogmouth occurs from sea-level up to 1500 m in New Guinea, and extends from its lowland rainforest strongholds into tall secondary forest and monsoon scrub, while there are a few Australian records of it in 20-year-old monocultures of *Araucaria*. The Papuan Frogmouth in New Guinea is found from sea-level to 1000 m, rarely ascending to 2250 m, and, besides the forest-edge and savanna habitats already mentioned, it ranges into second growth and urban gardens with trees. The wide habitat tolerance of the Tawny Frogmouth in Australia has already been noted, and its adaptability in colonizing urban gardens with trees is well known. It can also extend into rainforest regions where roads provide corridors of the open habitat it needs for hunting, bringing it alongside Papuan Frogmouths, but it does not commonly penetrate far into the rainforest interior that is occupied by Marbled Frogmouths.

General Habits

Frogmouths are secretive, nocturnal birds, and many of the species spend their entire lives in the understorey of dense forest, so it is hardly surprising that little is known of their habits. The best information is for the Tawny Frogmouth, which commonly lives in more open situations than all of the other members of the family, although even this species lacks any really thorough studies involving marked birds. The two other Australasian frogmouths, the Papuan and the Marbled, are considerably less well understood. In comparison with all the Australasian taxa, however, the



Frogmouths are masters of camouflage, as seen in this statuesque family group of Tawny Frogmouths. When alarmed, birds freeze into set positions so as to "become" ragged stumps of broken branches, their facial tufts aiding to break up the silhouette. Once the threat is over, the birds relax and assume less tense and upright stances. Tawny Frogmouths use a number of different daytime roost-sites, normally on branches, often in quite exposed positions. Though habitually alone or pairs, groups of up to five birds may roost communally, even side by side on the same branch, thereby taxing their powers of camouflage to the maximum.

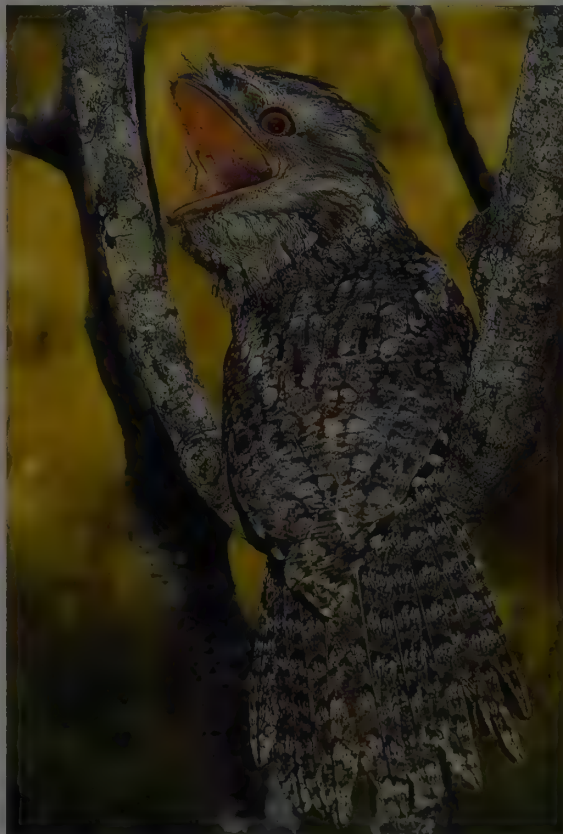
[*Podargus strigoides strigoides*, Whyalla, South Australia. Photo: Barry Silkstone/Nature Focus]

Asian *Batrachostomus* species are even more poorly known in life; most information is available for the Sri Lanka and Hodgson's Frogmouths, with scraps of data on several of the others, but nothing at all is recorded of the Dulit Frogmouth in the wild. This incompleteness of our knowledge must be borne in mind in the following generalizations, where every statement would otherwise need to be prefaced by a proviso such as "in those species for which information is available".

All data on frogmouths show or imply that they normally live in sizeable territories, which they advertise and defend with songs and threat calls. At least in the case of *Podargus*, a single male and a single female remain on the territory throughout the year. The pair-members often roost together, sometimes in side-to-side contact, although Marbled Frogmouths are reported more often to roost solitarily. Fledged young may remain on the territory for many months, sometimes until the next breeding season, and they may occupy daytime roosts near their parents, but all of the species essentially live solitarily or in pairs. Details of post-fledging care of the young and of their dispersal are mostly unknown. Scant data on the Sri Lanka Frogmouth suggest a similar pattern of social organization.

Daytime roosts are on stumps or branches of trees or saplings, sometimes in thickets. There are reports of the Marbled and Large Frogmouths roosting in tree holes, and use of holes might possibly account for the elusiveness of some of the species during the daytime, but other species in both genera are well known to roost on open perches. When disturbed by a human observer, the roosting bird normally remains motionless with its body held at an angle above the perch, the head erect, plumage sleeked, and eyelids almost closed over the eyes to leave just narrow slits. This "broken-branch" or freezing posture, coupled with the cryptic plumage coloration and choice of roost-site, usually renders the bird very inconspicuous, so that it often relies on its camouflage and allows the observer to approach closely. Some observers have been fooled into believing that a frogmouth approached in this manner is asleep, but the bird often follows their movements by slightly twisting its head, while its eyes are not totally closed; really close approach usually results in the bird flying away quickly and silently, or with a short call that may serve to warn its mate or young. A roosting bird can occasionally be caught by hand or with a hand-held net, especially when it is

on a nest or with young, but usually it will make off at the last moment. Very close approach by intruders, however, can at times result in a prolonged gaping threat display being directed at them; this display has sometimes been interpreted as feeding behaviour, and it is possible, but unproven, that a similar posture is occasionally used for feeding (see Food and Feeding). When the



If there is a suspicion of danger during the daytime the Tawny Frogmouth will freeze, relying on this posture, together with its cryptically patterned plumage and carefully selected roost-site, to remain inconspicuous. So confident is it of this camouflage that it will allow the close approach of an observer. The bird will eventually flush when the latter gets really near, flying off silently. However, on occasion the bird still holds its ground, and the unwanted visitor is subjected to a lengthy gape display, when the bill is opened to its maximum to ensure that the threat message is sufficiently clear!

[*Podargus strigoides brachypterus*, Perth, Western Australia. Photo: Peter Steyn/Ardea]

When trying to intimidate an opponent or a potential enemy, a frogmouth will fluff out its plumage, drooping the wings and fanning the tail in an attempt to look larger than it really is. A similar posture is frequently used for quite a different purpose, namely that of drying the plumage, as is perhaps best known in the cormorants (*Phalacrocoracidae*). Note the rather long central rectrices of this Papuan Frogmouth.

[*Podargus papuensis*,
Cape York Peninsula,
northern Queensland.
Photo: Hans & Judy
Beste/Ardea]



observer retreats a fair distance, the bird eventually relaxes its freezing posture and opens its eyes more widely. Incubating birds and those accompanying nestlings also use the freezing posture when intruders approach, and it is also adopted by fledglings of the Papuan Frogmouth and probably those of some other species. On the other hand, at least in the genus *Podargus*, birds

Although by far the best documented species in the family, the Tawny Frogmouth remains shy and secretive, and detailed descriptions of its comfort behaviour are few. One interesting activity, to date only observed in captive birds, is a form of rain-bathing. During a shower, the bird will lower its wings before raising them over its head, fluffing up its feathers, and then swaying from side to side. Meanwhile it droops its head low, and sometimes calls.

[*Podargus strigoides*
strigoides,
Lismore,
New South Wales,
Australia.
Photo: Roger Brown/
Oxford Scientific Films]



approached when they are perching at night do not adopt this posture, but merely fly away if the observer comes too close. After being disturbed during the daytime, *Podargus* frogmouths are sometimes mobbed by honeyeaters (*Meliphagidae*).

All frogmouths are essentially nocturnal in their activity. *Podargus* species are commonly most active for an hour or two after dusk and again before dawn, with a lull in the middle of the night. An account of the calling behaviour of Horsfield's Frogmouth also suggests a similar pattern of activity, which is common throughout the *Caprimulgiformes*.

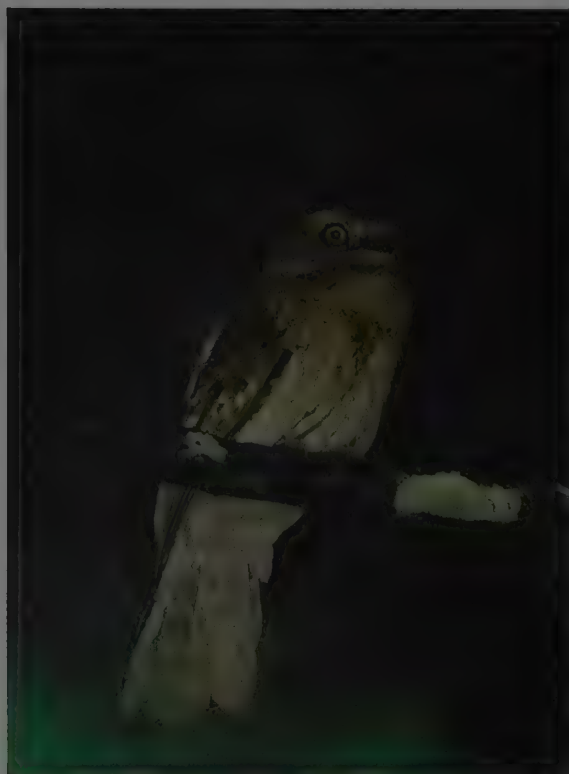
Very little is recorded of the displays and posturing of frogmouths, although vocalizations are evidently very important for signalling (see Voice). Tawny Frogmouths normally react to threats by flying away, but, if cornered, they are reported to fluff out their plumage, open their eyes wide and indulge in "frightening" bill-snapping that exposes the yellow gape (see Breeding). When Sri Lanka Frogmouths are disturbed at their daytime roosts, they are reported to bob the head two or three times before flying away.

Few data are available on the comfort behaviour of this family. Captive Tawny Frogmouths have been recorded sun-bathing while roosting on a branch or on the ground, prostrating themselves with outstretched wings and ruffled feathers. Allopreening has also been recorded for this species, paired birds at roosting sites preening themselves and each other about the head.

Voice

Frogmouths are often highly vocal, using "songs" to advertise and defend their territories, and uttering various other calls. For the ornithologist, the vocalizations provide the easiest means of locating and identifying most of the species, although those of the Dulit Frogmouth are still completely undescribed. The voices of several of the other *Batrachostomus* species are only partly known, while that of the Short-tailed Frogmouth has been described only very recently.

The large *Podargus* species have songs with a mellow hooting character, which may become more booming in quality at close range. Differences between their songs enable the three species to be readily identified: the ringing "coo-loo, coo-loo,



coo-loo, coo-loo, coo-loo" (4-7 phrases) of the Marbled Frogmouth is quite different from the soft "oom-oom-oom-oom..." (10-50 phrases) of the Tawny Frogmouth, or the very low-pitched, resonant "oom oom oom oom oom oom oom..." (9-13 phrases) of the Papuan Frogmouth. In all three species, both male and female sing, and in the case of both Marbled and Papuan Frogmouths the lower-pitched song is believed to be that of the female. Duetting by the two birds of a pair perhaps occurs in all three species. In any event, precisely timed antiphonal singing is reported for the Tawny Frogmouth, and songs of the Marbled Frogmouth are timed partly to overlap.

All three *Podargus* species typically sing from perches well up in trees, and Tawny Frogmouths often sing from the nest-site for long periods at the start of the breeding season. Tawny and Marbled Frogmouths may sing in many months of the year, but the song of the Papuan Frogmouth is reported to be given almost entirely in the breeding season.

These three species have several other calls that are used in territory defence, but the precise function of each of them is not well understood. As an example, studies of the Marbled Frogmouth at the Iron Range, Queensland, using playback of taped song, give some insight into the functions of song and other vocalizations. Initially, playback of such recordings is often answered from a distance by similar songs, which is in accordance with the likely role of the song in signalling the presence of territorial birds. Repeated playback of song within a territory may then lead to the pair of territory-owners approaching closely and repeatedly giving threat calls: each of them a quick series of gobbling units, becoming softer at the end and often terminating with a loud, sharp, mechanical bill-snap, "Wu-Wu-wu-w CLAK!". Prolonged taunting of the birds with further song playback may produce two other types of call: a rather soft, long, moaning hoot, "oooooooooooo...", and a quick succession of short, deep units, "to-to-to-to-to", both of uncertain significance. In addition to these calls and variants of them, the vocabulary of the Marbled Frogmouth is known to include a short trilling "brrr", a short barking "chuck" and, from the male and female feeding each other at the nest, soft squeaks, hisses and rasps. An account from New Guinea describes so-called "dual singing" lasting about 40 minutes from an adult and a fledgling, the adult giving a succession of low-pitched growls, and the young bird alternating with monotonously repeated "who" or "koooo" units. The signifi-

cance of this combined performance is uncertain but, contrary to the interpretation in the published account, it seems more likely to have involved repetition of begging and contact calls than a duetting territorial song involving a fledgling.

The vocabulary of the Tawny Frogmouth seems to be equally varied, with adults giving at least six types of call including the song, and even nestlings having numerous calls. A young bird hand-reared by Mrs F. Irby (see Relationship with Man) uttered at least seven types of call before fledging, including what was evidently the full song, "repeated sometimes an incredible number of times". In addition to those seven calls, large nestlings are reported to screech if alarmed.

Our understanding of the vocalizations of *Batrachostomus* species owes much to research by J. T. Marshall, which was carried out in parallel with his studies on the small owls of South-east Asia. He used song types in conjunction with plumage and other characters to clarify the taxonomy of several of the species. The smaller *Batrachostomus* species whose vocalizations are sufficiently well known have short, whistled or rather harsh songs, the main territorial song apparently being given by the female and a different, often less noticeable song (or call) by the male. Thus, in the Philippine Frogmouth, the female utters a single falling note like that of the Indian Scops-owl (*Otus bakkamoena*), and the male a faint trill; the female Hodgson's Frogmouth gives a single long whistle which rises and then falls in pitch, whereas the male has short calls; in Horsfield's Frogmouth, the female gives a descending "qwaa-qwaa-qwaa-qwaa" series sounding like maniacal laughter, while the male utters a plaintive single whistle. The songs of the other species are less well understood: for the Large Frogmouth, a deep, hollow-sounding tremolo and a loud wheezy call have been described; in Gould's Frogmouth, the male's song is a whistled "oooh-wheeow"; Sri Lanka Frogmouths give a soft, rapid "koooo, koooo, koooo"; and the song of a presumed female Sunda Frogmouth is a descending series of "qwaa" units, all starting on the same pitch and sounding like the "caw" of a Large-billed Crow (*Corvus macrorhynchos*). In addition to the main song or call of each sex, several other calls have been described for some of the species, but the catalogue of these is still very incomplete, and the behavioural contexts and functions of those that have been tape-recorded or described is largely unknown.

Food and Feeding

There has been no detailed study of the diet of any frogmouth, although considerable information on gut contents of adult birds



Basing themselves on the frogmouths' huge bills, early naturalists assumed that they caught their prey in mid-air like flycatchers. It now appears, however, that such behaviour is rare, and for the most part they capture insects and other food items by seizing them with the bill either on the ground or off trees. There is, in fact, a record of a Gould's Frogmouth snapping at insects in the air, and maybe this technique is more widespread than currently thought, at least in *Batrachostomus*, with their somewhat smaller bills. Note the forward facing, rather owl-like eyes of this individual.

[*Batrachostomus stellatus*, Way Kambas, southern Sumatra. Photo: Bill Simpson]

While insects form the bulk of the diet of all frogmouths, the large *Podargus* species will feed on small vertebrates as well, thanks to the huge size of their bills, as demonstrated by this Tawny Frogmouth. Such prey is often given a vigorous thrashing against the perch to ensure tenderness before it is swallowed at one gulp.

[*Podargus strigoides*, Queensland, Australia. Photo: W. K. Clifford/Nature Focus]

Tawny Frogmouths invariably build their loose, platform-like nest of small twigs and sticks some 1-7 m above the ground, in the fork of a tree. Both sexes participate in the nest building, which can take a month to complete. The material is collected from trees and shrubs, the birds breaking off twigs with their bills in flight. Material is constantly added during the few days after the eggs have been laid, and is frequently rearranged during incubation. The male is known to sit during the day, while the female roosts in a nearby tree; at night they take turns on the nest.

[*Podargus strigoides*,
Australia.
Photo: Ford Kristo/
Planet Earth]



has accumulated for the *Podargus* species and sparser data for most, but not all, of the *Batrachostomus*. Insects, particularly large ones, are the prey items most often reported. Of these, beetles (Coleoptera) and grasshoppers and their relatives (Orthoptera) are the commonest groups, although their prominence in lists may reflect their ease of identification for ornithologists who are not expert entomologists as much as it does their frequency as prey. Other insect groups recorded include Blattodea (cockroaches), Dermaptera (earwigs), Hemiptera (bugs), Hymenoptera (wasps, bees, ants), Isoptera (termites), Lepidoptera (moths and their larvae), Mantodea (mantids), Neuroptera (lacewings), Odonata (dragonflies) and Phasmatodea (phasmids). Records of small invertebrates other than insects include spiders, myriapods (centipedes, millipedes), scorpions, crustaceans (Decapoda), earthworms and, rarely, slugs and snails.

Small vertebrates have also been recorded as prey of *Podargus*, but not of the mostly smaller *Batrachostomus* species. These vertebrate prey include frogs, taken by all three *Podargus* species, with lizards, small rodents and occasionally small birds represented in the diet of the larger Papuan and Tawny Frogmouths. Among the larger vertebrate prey taken by the Tawny Frogmouth are records of the House Mouse (*Mus musculus*), House Sparrow (*Passer domesticus*) and Brown Treecreeper (*Climacteris picumnus*). This species is reported also to exploit plagues of mice, but not to feed on carrion. Captive birds kept in England in the nineteenth century regularly ate strawberries and other soft fruits; similar foods have not been recorded in the wild, although few of them are available in this species' natural range and habitat. In northern Australia its diet is thought to include a large proportion of insects at all times of the year, but in the south a shortage of insects in winter is believed to force the birds to take more arachnids and myriapods.

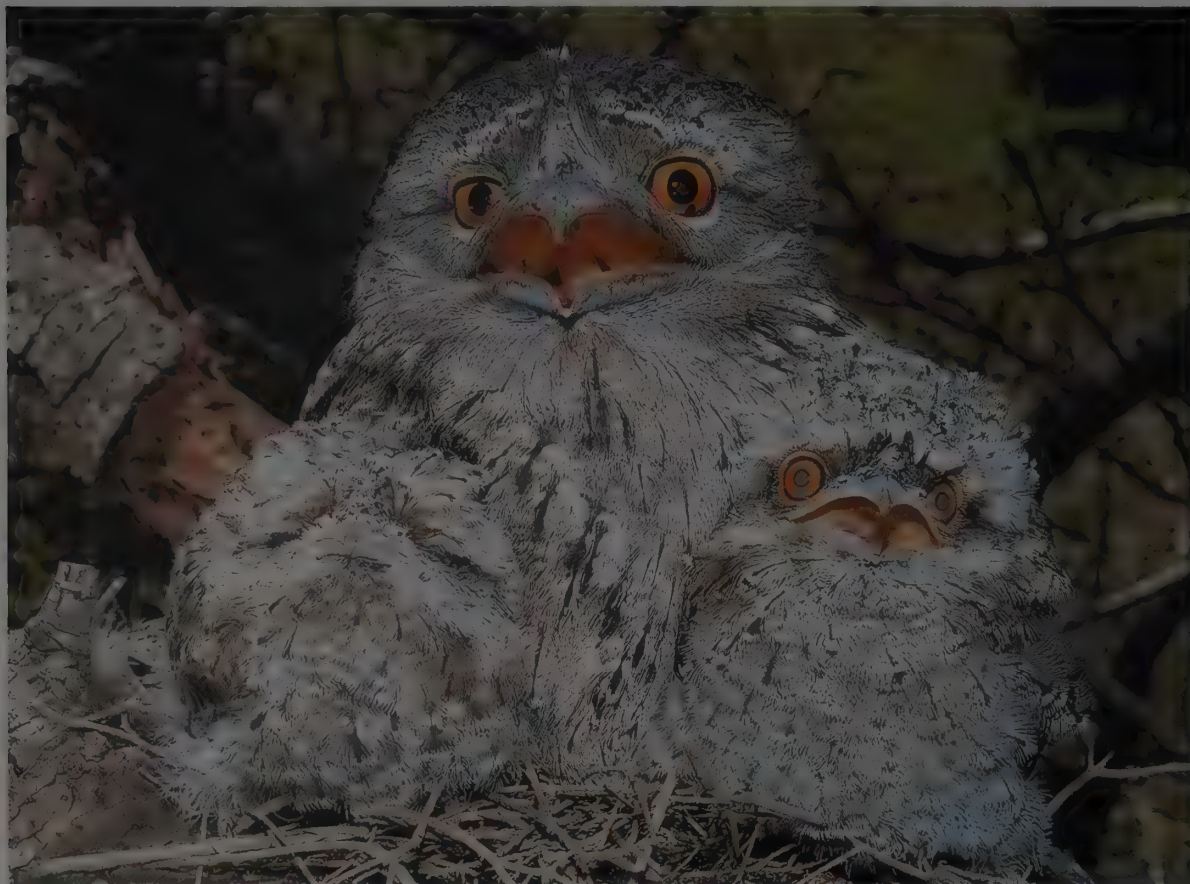
Because of the difficulties of making direct observations at night, not much is known of the hunting behaviour of *Podargus* and very little information exists on that of any of the species of *Batrachostomus*. The predominant feeding technique, however, appears to consist of sallying from a prominent perch to catch

moving insects and other prey. Food is taken mainly from the ground by the Tawny Frogmouth, which usually hunts in clearings, but more often from trunks, branches or foliage by Horsfield's Frogmouth and perhaps other *Batrachostomus*. Records of flightless prey, such as caterpillars or wingless beetles, also imply that prey-capture occurs on the ground or on trunks or foliage. Indeed, despite some earlier accounts, there is little evidence of insects being captured in flight by *Podargus* species, although rare instances of such behaviour are known for the Tawny Frogmouth. M. Bartels, however, surmised that Horsfield's Frogmouth catches some prey, such as moths and alate termites, on the wing in flycatcher-like flights.

At least in the case of *Podargus* species, prey is captured in the bill, small items being swallowed immediately. Large or hard prey are carried back to the perch, where they may be shaken, mandibulated or bashed against the perch to render them easier to swallow. There are clear descriptions of a captive Tawny Frogmouth "beating mice to a pulp with its beak before swallowing them at a gulp", and of a baby mouse being "shaken to and fro with the obvious view of killing it and breaking its bones" before it was swallowed. The stronger bill of frogmouths compared with other Caprimulgiformes enables them to take tougher prey, including large, hard beetles and small vertebrates, than could be readily consumed by a *Caprimulgus* nightjar. The food-bashing behaviour of the *Podargus* frogmouths doubtless adds further to this ability, and the presence of digestive grit presumably also aids in comminuting hard food.

An intriguing record exists of apparent opportunism in foraging behaviour, also involving kleptoparasitism. This consists of a single report of a Papuan Frogmouth stealing a green tree-skink (*Dasia*) from the beak of a Helmeted Friarbird (*Philemon buceroides*), an event which occurred in the daytime.

There has been interesting speculation recently about the use of open-mouthed flycatching postures by species of both genera. Two tribesmen in Papua New Guinea reported to J. M. Diamond that the Papuan Frogmouth "sometimes sits with its mouth wide open for long periods, with a sticky substance on its palate that



Tawny Frogmouth chicks are semi-altricial and are brooded on the nest for two or three weeks. As with incubation, the daytime stint is normally taken by the male. What happens at night, however, is not well known. It is thought that both sexes take turns, but it is not clear whether there is a strict alternation of bouts, or a less rigid pattern with both sexes participating for parts of the time. Difficulties of sexing birds in the wild, especially at night, probably hinder precise conclusions being drawn from the observations.

[*Podargus strigoides*
strigoides,
Gympie,
south-east Queensland.
Photo: Cyril Webster]

might serve to attract or trap insects". Diamond later elaborated on this to suggest that the probable reason why the birds use the open-mouthed posture is that they secrete a smelly, sticky saliva inside the mouth which acts as a chemical bait and lures insect prey. R. Kannan was inclined, reasonably enough, and on the basis of his observations of gaping by Sri Lanka Frogmouths, to reinterpret these reports as being instances of gaping threat displays that had been misunderstood by the observers. Nevertheless, an early and hitherto overlooked account by Mrs Irby (see Relationship with Man) of a hand-reared fledgling Tawny Frogmouth suggests that Diamond's interpretation merits further study, especially as another overlooked old account by E. Coleman describes similar behaviour by adults of this species. Mrs Irby recorded that her fledgling "loved to sit still in the evening with his mouth wide open, shutting it with a loud snap if a mosquito or any small insect flew in".

Breeding

Unlike most caprimulgiforms, frogmouths build well-formed nests that are usually placed on branches of trees, shrubs or saplings, or sometimes on top of an epiphyte or on an old nest of some other bird species. Tawny Frogmouths may use the same nest-site repeatedly, even when nesting attempts fail, and one site was known to have been used for 21 years in succession. There is no comparable information on the re-use of nests by the other species.

The structure of the nest differs considerably between the two genera. The nest of *Podargus* species is a bulky to rather small platform of criss-crossed twigs, thin sticks, vine tendrils or plant stems, sometimes incorporating small amounts of grass culms, leaves, moss or lichen, and with a shallow cup; measuring about 10-26 cm across by 4-10 cm deep in the Tawny Frogmouth, for example, it is reminiscent of a bulky nest of a pigeon (Columbidae). The Marbled Frogmouth is reported to build smaller nests than those of its two congeners, more like the small cups of drongos (Dicuridae) than twiggy platforms; some are little more than a depression in the moss on a horizontal bough.

Although the nests of several *Batrachostomus* species are still unknown, it seems unlikely that they will be found to differ much from those of their congeners which have been described. These species build a very small, neat, firm cup that consists mainly of interwoven down plucked from the birds' own underparts, with small amounts of cobwebs, mosses, lichens or leaves; the last four materials are mainly on the outside, and serve to conceal the nest rather than contributing much to the structure. The Sri Lanka Frogmouth's nest is about 5.7-6 cm across and 3.7 cm deep at the sides, but only 1.3 cm deep in the centre. It is likely that the proportionately tiny nests of *Batrachostomus* and the small nest of the Marbled Frogmouth have been evolved to reduce predation. They are extremely well concealed, in contrast to the more substantial twiggy nests of Tawny and Papuan Frogmouths, but the latter are the two largest species of the family and therefore less likely to be at risk from predators.

Both sexes of the Tawny and Marbled Frogmouths are known to collect nest material by breaking or pulling it from trees and shrubs, and sometimes, in the case of Tawny, also from the ground. Both sexes incorporate material into the nest. For the Papuan Frogmouth, it is recorded that each member of the pair "takes turns" in breaking off twigs in flight and bringing them to the nest-site, while the other works them into the nest. Nest-building is reported to take about a month in the Papuan Frogmouth, whereas Tawny Frogmouths usually take two to four weeks, although they can apparently build a nest completely in several nights; some addition and rearrangement of material continues during incubation. Hardly anything is known of the nest-building behaviour of the *Batrachostomus* species, although nests of Hodgson's Frogmouth are reported to include down from the underparts of both male and female adults.

In the family as a whole, clutches are mainly of one or two eggs, but those of the Tawny Frogmouth sometimes consist of three and rarely of four, or perhaps even five. The commonest clutch of both Papuan and Marbled Frogmouths is one egg, with two being rare or infrequent; in the Marbled Frogmouth, normally only one nestling is reported, even from two-egg clutches.



For the most part, the *Batrachostomus* species breed in thick primary forest vegetation, and, perhaps as a consequence, the nests of some species have yet to be described.

The Sunda Frogmouth builds what is reckoned to be a typical *Batrachostomus* structure, flimsily made of soft down, lichens, pieces of bark and cobwebs, forming a shallow cup, and placed on a horizontal branch close to the trunk.

Unlike its congeners, it shows a preference for nest-sites in secondary growth on the edge of primary forest, and in Brunei nests have even been found in exotic trees in suburban gardens.

Not unexpectedly, considering the size of the nest, the clutch consists of a single egg.

The precarious nature of the nest implies that the adults must exercise great care in both incubating and brooding to avoid accidents.

[*Batrachostomus cornutus*
cornutus,
Brunei.

Photo: Hans Christian
Heap/Planet Earth]



In the Tawny Frogmouth, the male is thought to play no part in feeding the chicks for the first two or three weeks. Very small chicks will beg for food by opening the gape wide and rocking to and fro. When older they simply reach up to take food proffered to them by the parents. When first hatched, the nestlings are covered in long white down, which is replaced after about a week by a second coat of down, this time greyer with white flecks and bars. The droppings of the young are removed for the first ten days, after which the chicks begin to defecate over the side of the nest.

[*Podargus strigoides*
strigoides,
Gympie,
south-east Queensland.
Photo: Cyril Webster]

There are apparently also interesting differences in clutch size among the species of *Batrachostomus*, so far as the limited information available allows generalizations. The two species for which nesting is best known are the Sri Lanka Frogmouth, which lays a single egg, and Hodgson's Frogmouth, which normally lays two (smaller) eggs but sometimes only one. Among the poorly known species, two-egg clutches are reported for Horsfield's, but only single eggs for Large, Philippine, Gould's, Short-tailed and Sunda Frogmouths. Laying by the Tawny Frogmouth is reported to occur at intervals varying from one to three days, but no comparable data are available for other species. The eggs are pure white and ellipsoidal, with a fine-textured surface that has only a slight gloss. They vary in size from 43-55 x 30-36 mm in the Papuan Frogmouth to 23-25 x 16-18 mm in the smallest race, *affinis*, of Horsfield's Frogmouth.

Incubation during the daytime appears to be undertaken exclusively by males. Involvement of the female in incubation at night has been established for Hodgson's Frogmouth, which sits during evening twilight and for one to two hours before dawn, and probably also for the Sri Lanka and Tawny Frogmouths, so this arrangement may apply to all species. In the Tawny Frogmouth, incubation begins when the first egg is laid, resulting in asynchronous hatching. In the genus *Podargus*, the incubating bird is fed on the nest at night by its mate, but there is no information on whether this applies also to *Batrachostomus*. The nests of *Batrachostomus* are so tiny in relation to the size of the egg that several observers have wondered how the egg remains in the nest. Since no adhesive is involved, it seems likely that arrangements are much as those adopted in roughly similar circumstances by the White Tern (*Gygis alba*); that species lays on a bare branch, with the egg never being left untended by the adult birds, and any change-overs during incubation being carried out carefully. Incubating males of species of both frogmouth genera are described as remaining motionless and always steadfastly facing in the same direction, so this behaviour may serve to reduce the chances of eggs being accidentally dislodged, as well as reducing losses to predators. Observations from hides at Tawny Frogmouth nests show that the male turns the eggs no more than once every 12 hours. This is the only species for which the incubation period has been recorded, with a duration of usually 30 days but ranging from 28 to 32 days.

In the Tawny Frogmouth, small young are brooded by both parents "alternately" for two to three weeks, and the adults are reported sometimes to help hatchlings out of the eggshell. The chicks' droppings are removed for the first 10-11 days, after which the young defecate over the side of the nest. The small chicks are reported to receive food only from the female, but this requires confirmation since it is well known that older young are fed by both parents, each of them bringing food separately to the nest. Small nestlings beg by raising the wide-open bill and making rocking movements; larger young reach up and take food held over them by a parent. Sparse information on the Papuan Frogmouth suggests that parental care in that species may be similar to that exhibited by the Tawny Frogmouth, but there is no information for most other frogmouth species.

It is clear that nestlings of all three *Podargus* species bear two successive downy plumages. In this respect they resemble the owlet-nightjars, but differ from the true caprimulgid nightjars, which have only a single down plumage. The Tawny Frogmouth nestling hatches in the first down, which is white and up to about 15 mm long; by about the seventh day this is being replaced by the second down, which is long and grey, with white flecking and barring, and paler on the underparts. Some of the second down remains on the body at fledging, being lost progressively until, by the third or fourth week, it is present only on the underparts; by the time the young are able to fly strongly, the last vestiges of down are visible about the carpal joint and the base of the underwing. The sequence is apparently similar in the Marbled and Papuan Frogmouths. Data on *Batrachostomus* nestlings are too limited for it to be said that they also have two successive down plumages, although this seems likely since the Sri Lanka Frogmouth is described as having pure white down (first down?), whereas the skin of a bird near fledging has the remaining (second?) down rufous-buff, paler beneath, with narrow darker barring. It appears reasonable to speculate that the function of the white first down of frogmouths is to make the small young conspicuous to their parents so that they are not accidentally dislodged from the nest, while the near-constant brooding of small young leaves little risk of their being seen by predators. The duller coloration of the second down presumably reduces the risk of predation, which might otherwise be high because the parents cease brooding when young are well grown.

The fledging period in the Tawny Frogmouth is 25-35 days. After leaving the nest, the young are fed by their parents for a further one or two weeks and remain with them for several months longer, sometimes until shortly before the next breeding season. The Papuan Frogmouth appears to be similar in this aspect of its biology, but there are no data for other species.

The anti-predator behaviour of incubating adult males and those tending small young appears to be designed entirely to promote concealment, with the "broken-branch" or freezing posture (see General Habits) being adopted when intruders appear. At such times the bird can often be caught by hand at the nest, and it gives no special display if approached very closely, relying on crypsis until it flees at the last possible moment. The two largest species, however, the Papuan and Tawny Frogmouths, are sometimes more aggressive in defence of their young, although such behaviour has not been reported for any of the smaller species. Papuan Frogmouths, if threatened when with young, may gape, hiss and snap the bill, or flutter at the intruder while bill-snapping. Tawny Frogmouths disturbed when brooding young may adopt a defensive-threat posture, fluffing their feathers, spreading the wings and tail, snapping the bill and clucking and hissing.

As with adults, the anti-predator behaviour of well-grown nestlings also consists mainly of promoting concealment by remaining silent and adopting the "broken-branch" posture. A large nestling Tawny Frogmouth, however, when threatened, had "the extraordinary ability to make himself uncannily grotesque", puffing itself out like a ball of fluff, giving growling and quick, repeated "too-too-too-too..." calls, drawing itself out to its full length, bending low, and swaying in a most curious manner as it called!

Movements

Although they can fly strongly, frogmouths appear to be among the most sedentary of all birds. No species is migratory; in-

deed, none is known to make even local seasonal movements. A possible sighting of the Tawny Frogmouth was reported from near Morehead in southern Papua New Guinea, but there is no confirmed record of extralimital vagrancy by any member of the family. Adults of at least the three *Podargus* species apparently remain in their territories throughout the year, although these may in extreme cases span a kilometre or two. Published statements that Tawny and Papuan Frogmouths are partial migrants appear to be erroneous. Nevertheless, some dispersal of at least young birds must surely occur, although this has not yet been documented.

While some records of frogmouths from hitherto unknown localities could be the result of short-distance movements, in many cases it seems far more likely that the birds had simply been overlooked in the area before. For example, a Horsfield's Frogmouth discovered in April 1997 in Cochinchina was apparently the first record of that species for Vietnam; the relatively widespread but fragmented distribution of Horsfield's Frogmouth, however, makes it very probable that it had always been present in that part of Vietnam but had long remained undetected.

Relationship with Man

Because most frogmouths are unobtrusive and nocturnal forest birds they are commonly overlooked, even by local people. Tribesmen in New Guinea know them and give accounts of their behaviour, although it is unclear how much in what they report is based on astute observation and how much may be surmised or possibly derived from superstitious beliefs (see Food and Feeding). European settlers in Australia became acquainted with Tawny Frogmouths, but it is quite evident from the names they used for these birds, such as "Mopoke" and "Morepork", that the species was extensively confused with the common small owl of Australia, the Southern Boobook (*Ninox boobook*).



The Tawny Frogmouth is thought to lay its eggs at intervals of 1-4 days, and asynchronous hatching may explain the marked size difference between these two chicks. Shortage of food often leads to the smaller, weaker chick being fed less regularly, so that it develops more slowly or may even finally die of starvation. After the young leave the nest, the parents continue to feed them for about two weeks, remaining to roost with them at or near the nest. Eventually, the family group will move to another roost site within the territory. Though the adults cease attending their offspring after six weeks, they will all stay together for several months until the time comes to disperse.

[*Podargus strigoides*,
Australia.
Photo: John Young]



The true status of most frogmouth species is very difficult to gauge, given their furtive habits which mean that most are almost certainly under-recorded in surveys. Nevertheless, it is probably true to say that most species have suffered notable declines, as wholesale logging has repeatedly made inroads on their preferred habitats. The Sri Lanka Frogmouth, with its rather small range in southern India and Sri Lanka, is currently classed as Near-threatened.

Although it regularly uses second growth and bamboo thickets, habitat loss appears to be the chief threat facing it.

[*Batrachostomus moniliger*,
Sinharaja, Sri Lanka.
Photo: Bill Simpson]

Members of the genus *Podargus* are occasionally kept in captivity in zoological gardens, and the Tawny Frogmouth has bred in captivity in Australia and in Europe. The other species, however, are very rarely represented in collections of captive birds.

In the 1920's, the chance find of a Tawny Frogmouth nestling blown from its nest onto the ground by high winds and its subsequent hand-rearing by Mrs Irby led to a remarkable account of this bird's development and behaviour being published in the *Emu*, the journal of the Royal Australasian Ornithologists Union. Although written in a sentimental style that differs radically from that now used in the *Emu* and other modern ornithological publications, Mrs Irby's record of her frogmouth remains to this day unsurpassed for some details of the species' behaviour and voice.

Status and Conservation

None of the frogmouths appears in the lists of internationally threatened birds, although the Large, Dulit and Short-tailed Frogmouths are classed as Data-deficient species, the small geographical ranges of the latter two implying that they are especially vulnerable in a region where extensive forest destruction is occurring. Nevertheless, many of the species have undergone considerable reductions in range, with numerous local populations being lost or greatly threatened. The main reason for these declines is the radical degradation and fragmentation of rainforest, primarily as a consequence of logging. Since the majority of frogmouth species live in rainforest, most of them are inevitably declining as a result of this destruction of their habitats, although only for a few species have losses been well documented.

Of these, the Marbled Frogmouth in north-east Australia has given particular cause for concern, especially with regard to its southern race *plumiferus*. Recent surveys have found this form to be present at 250 sites, but within its range it is mostly restricted to tiny fragments of forest. Although not in immediate danger of extinction, it must still be regarded as one of the rarest birds in Australia, and one that will require careful monitoring if its survival is to be assured. The Sri Lanka Frogmouth of southern India and Sri Lanka has also decreased owing to forest destruction. In the Western Ghats of India, a survey in Kerala State

found 34 birds and reported that, while the species was uncommon, it did not appear to be endangered. Although the Sri Lanka Frogmouth is widespread in its namesake island, it is apparently scarce and is present only in small numbers in most regions. Nevertheless, since it occurs there in a variety of well-wooded habitats, and not just in the lowland rainforest of the south-west of the island, it is probably less immediately threatened by destruction of rainforest than are those Sri Lankan endemics which are restricted to that habitat.

The long-term survival of some of the species of rainforest-inhabiting frogmouths must depend on protection of sufficiently large areas of primary forest in which even selective logging is prevented, but a much wider importance is attached to the conservation of these habitats, of course, for their endemic biota and for other reasons. It would, however, be valuable to have much more detailed information than currently exists on the location and sizes of populations of frogmouths, especially the scarcer species such as the Dulit and the Short-tailed, as well as those which are restricted to the "best" rainforest habitats, such as the Large Frogmouth. In order for this information to be gained, it will be necessary to discover more about the vocalizations of all three of those species, and then to carry out extensive nocturnal surveys.

The only species of the Podargidae that appear to be exempt from losses brought about by destruction or degradation of forest are the three that live in other habitats, namely the Tawny and Papuan Frogmouths and, probably, the Sunda Frogmouth. The Tawny Frogmouth appears to be particularly resilient, having colonized suburban gardens and farmland with trees, and having withstood heavy mortality caused by road traffic and predation by introduced cats and foxes.

General Bibliography

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PLATE 23

inches 6
 cm 15



Family PODARGIDAE (FROGMOUTHS) SPECIES ACCOUNTS

PLATE 23

Subfamily PODARGINAE

Genus *PODARGUS* Vieillot, 1818

1. Marbled Frogmouth

Podargus ocellatus

French: Podarge ocellé **German:** Marmorschwalm **Spanish:** Podargo Ocelado
Other common names: Little Papuan Frogmouth; Plumed Frogmouth (*plumiferus*)

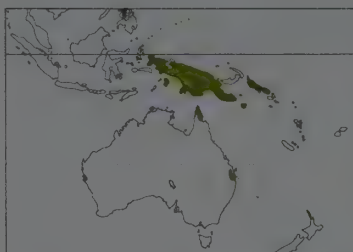
Taxonomy. *Podargus ocellatus* Quoy and Gaimard, 1830, Manokwari, New Guinea.

Plumage coloration and rainforest habitat differ from those of congeners, and may suggest some distant affinity with *Batrachostomus*; although these similarities may be at least partly due to convergent evolution; race *inexpectatus* of Solomon Is shows strong superficial resemblance to *Batrachostomus auritus*, although differs in structural details and lacks white hindneck-collar. Taxonomy of southernmost race *plumiferus* much confused in past, partly because of dearth of available specimens, leading to over-reliance on descriptions; it has been treated as a race of *P. papuensis* or of *P. strigoides*, but recent study of specimens and vocalizations leaves little doubt that it is best regarded as a race of present species. Six subspecies currently recognized.

Subspecies and Distribution.

P. o. ocellatus Quoy & Gaimard, 1830 - New Guinea, Aru Is, W Papuan Is and islands in Geelvink Bay.
P. o. intermedius Hartert, 1895 - Trobriand Is and D'Entrecasteaux Is.
P. o. meeki Hartert, 1898 - Tagula I (Louisiade Archipelago).
P. o. inexpectatus Hartert, 1901 - N Solomon Is (Bougainville, Choiseul, Santa Isabel).
P. o. marmoratus Gould, 1855 - Cape York Peninsula (N Queensland).
P. o. plumiferus Gould, 1846 - coastal E Australia from SE Queensland to NE New South Wales.

On following pages: 2. Papuan Frogmouth (*Podargus papuensis*); 3. Tawny Frogmouth (*Podargus strigoides*).



Descriptive notes. 37–48 cm; 132–180 g (*ocellatus*). Plumage coloration variable; some accounts refer to distinct colour morphs, but variation in coloration appears to be continuous between the extremes. General colour of male's upperparts ranges from dull grey-brown (often with intricate marbling and streaking) to deep rufous (often with very little marbling and few dark spots and streaks); underparts also variable, but most often with irregular whitish barring and longitudinal streaks of dark brown and blackish. Distinguished from *P. strigoides* most reliably by longer tail and different vocalizations; *P. papuensis* is much

larger, with different song. Female often darker than male, but not always separable. Juvenile not well described, but reported as rufous-brown, faintly barred white and tipped dusky on head and underparts, faintly barred dusky on back and mantle. Races differ mostly in size and details of coloration; *inexpectatus* is the most distinctive, with finer dark markings on upperparts and clear white spots on wing-coverts. **VOICE.** Highly vocal; frequently calls from perch in tree. Territorial song consists of phrase of 4–7 "coo-loo" units repeated in quick succession; threat call a quick series of gobbling units that often terminate with loud, mechanical bill-snap.

Habitat. Humid forest; in addition to rainforest, also occurs at forest edge, and in tall secondary forest and vine forest. Two unusual records of race *plumiferus* inside 20-year-old monocultures of hoop pine (*Araucaria cunninghamii*). Mainly in lowlands, but recorded up to 800 m in Australia and to 1500 m in New Guinea.

Food and Feeding. Diet consists mainly of large insects such as beetles and grasshoppers, with a single report of a frog being eaten. Hunts by hawking from prominent perch, typically within several metres of ground in forest substage, taking prey on the ground, foliage, branch or tree trunk after a shallow, diving glide; prey captured in bill. Large or hard items may be carried back to perch and battered vigorously before being eaten.

Breeding. Aug–Dec (–Feb) in Australia; few data from New Guinea suggest Mar, May, Aug–Nov; large nesting on Bougainville in Aug. Presumably single-brooded. Nest is a small, flat or shallow platform of twigs, vine tendrils, moss, etc., placed 3–15 (–25) m above ground on flat tree-fork or on crown of epiphyte. Clutch 1 egg, infrequently 2; incubation and fledging periods unknown; both sexes apparently share incubation and care of young, with confirmation from collected birds that males incubate and tend young during day; nestling has white first down. It is reported that usually only single young fledges from nests on Cape York Peninsula, even with 2-egg clutches.

Movements. Adults are apparently sedentary in territories throughout year. No information on dispersal or other movements of young birds.

Status and Conservation. Not globally threatened. Status of both subspecies in Australia gives cause for concern, since they depend on rainforest fragments. In particular, *plumiferus* has declined greatly owing to widespread destruction of its forest habitat for agriculture, grazing, and timber production, with the result that it is now a rare bird that will require careful monitoring in future; although a recent survey found it at 250 sites, many of these are in tiny fragments of forest that support very small numbers. Solomon Is race *inexpectatus* was reported to be uncommon in 1981.

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2. Papuan Frogmouth

Podargus papuensis

French: Podarge papou **German:** Papuaschwalm **Spanish:** Podargo Papú
Other common names: Giant/Great (Papuan) Frogmouth, Large Frogmouth(!)

Taxonomy. *Podargus papuensis* Quoy and Gaimard, 1830, Manokwari, New Guinea. Considerable geographical variation in size in New Guinea region, but chequerboard pattern of distribution of large and small birds makes recognition of races impractical. Although two races recognized in Australia by some recent authors, with a larger, paler form on Cape York Peninsula (*rogersi*) and a smaller, darker form in coastal NE Queensland S of Cooktown (*baileyi*), Cape York birds appear indistinguishable from those of S New Guinea and some characters of *baileyi* can be matched by certain New Guinea populations. Monotypic.

Distribution. New Guinea, W Papuan Is, islands in Geelvink Bay and Aru Is, and NE Australia in N & E Queensland (Cape York Peninsula S to R Staaten and Paluma Range).



Descriptive notes. 45–60 cm; 256–599 g. Largest of genus, with long tail; coloration rather variable, and some birds much darker than others. Male's upperparts generally appear grey-brown, but in detail have elaborate light and dark pattern; underparts generally light brown-grey, with spots and short irregular bars of white, and variable blackish streaking; irides frequently bright red, but often orange, yellow or brown. Iris colour, when red, a useful distinction from congeners. Female much like male and similarly variable, although typically with more brown or rufous tone, especially on upperparts, and less contrasting light and dark markings; rarely, female (but apparently not male) occurs as "rufous morph", almost entirely plain cinnamon. Juvenile coloration evidently very variable, from generally similar to adult to much paler, with underparts mainly white. **VOICE.** Reported to be vocal virtually only when breeding. Territorial song a low-pitched, resonant series of 9–13 units, "oom oom oom..."; several other calls are made, in addition to mechanical bill-snapping.

Habitat. In New Guinea, inhabits savanna with trees, rainforest (mainly at edge), second-growth woodland, gallery woodland, groves of trees, scrub and urban gardens; from sea-level to 1000 m, rarely to 2250 m. In Australia, occurs mainly in lowland areas, on edge of rainforest, in rainforest-scrub, vine forest, gallery and paperbark (*Melaleuca*) forest along streams, some *Eucalyptus* woodlands, swamp-woodland and mangroves.

Food and Feeding. Diet consists mostly of large beetles and grasshoppers, but also includes other insects, spiders, myriapods, snails, lizards, rodents and even small birds. Hunts by sallying from a prominent perch, such as a low bare branch, stump or fence, planing down in a shallow, noiseless glide to catch prey in the bill; a single report of a green tree skink (*Dasia*) snatched from the beak of a Helmeted Friarbird (*Philemon buceroides*) in daylight. Large and hard prey items are carried back to the perch and bashed and crushed before being swallowed.

Breeding. Season in Australia Jul–Feb, mostly Aug–Dec, with peak Oct–Nov; incomplete information from New Guinea suggests laying mainly in dry season, e.g. at least Jul–Nov in Port Moresby region, with adults on nests in Oct and Nov on N coast, and fledgling on Misool in Jan. Single-brooded (Australia). Nest is a rough platform, rather scanty or substantial, of criss-crossed twigs, placed on horizontal fork of tree mostly 6–20 m (2.4–36 m) above ground. Clutch 1 egg, rarely 2; probably both sexes incubate, although only males have been collected from nests during the day; incubating bird always faces in same direction on nest, and at night one of pair constantly feeds and attends the other; incubation period not reported; nestling has white first down, whitish-fawn to fawn second down; young fed by both adults alternately, at least when small; fledging period unknown; fledged young begin to fend for themselves about 1 month after leaving nest, but may remain with parents almost until beginning of next breeding season.

Movements. Although some Australian literature suggests that species is migratory, this is based on old anecdotal accounts that were probably mistaken. Adults occupy the same territory throughout year. No information on dispersal of young birds.

Status and Conservation. Not globally threatened. Apparently remains common in parts of its limited Australian range; in New Guinea generally not uncommon, and locally fairly common (e.g. in Varirata National Park). Unlike many Australian rainforest birds that have declined as a result of habitat loss, it can tolerate some clearing and agricultural development, and is therefore still present over much of its historical range.

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3. Tawny Frogmouth

Podargus strigoides

French: Podarge gris **German:** Eulenschwalm **Spanish:** Podargo Australiano
Other common names: Freckled/Tawny-shouldered Frogmouth, Mopoke, Morepork(!), Night Hawk, Podargus

Taxonomy. *Caprimulgus strigoides* Latham, 1801, New Holland = Sydney, New South Wales. Possibly the most divergent member of the genus; coloration, proportionately long and pointed wings, short tail and strong feet are all adaptations to its relatively dry woodland habitat. Wide individual and sexual, as well as geographical, variation in coloration and size led to naming of numerous races in past; proposed races *lilae* (Groote Eylandt) and *gouldi* (NE Australia) included in *phalaenoides*, while *cornwalli* (E Queensland), *victoriae* (SC Australia) and *cuvieri* (Tasmania) all now lumped into nominate; much of the variation now known to be clinal, resulting in various recent treatments reducing number of valid races to five, three, two or none, but detailed studies now indicate three should be accepted. Three subspecies currently recognized.

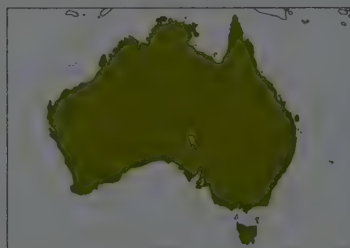
Subspecies and Distribution.

P. s. phalaenoides Gould, 1840 – throughout N Australia, S to Great Sandy Desert, Barkly Tableland and S plains of Gulf of Carpentaria in Queensland.

P. s. brachypterus Gould, 1841 – Western Australia (N to Great Sandy Desert) NE to Channel Country of Queensland and SE to Murray mallee in Victoria.

P. s. strigoides (Latham, 1801) – E & SE Australia (S from N of Cooktown, W to inland fringes of Great Dividing Range and SE South Australia) and Tasmania.

A single unconfirmed sight record (subspecies uncertain) from near Morehead in S Papua New Guinea.



Descriptive notes. 34–53 cm; 205–364 g (*phalaenoides*), 180–680 g (*strigoides*). Coloration very variable, but upperparts normally greyish, boldly streaked black, with intricate finer barring and vermiculation; underparts pale greyish, with thin to strong blackish streaks, variable brown to rufous suffusion and variable amounts of irregular white barring. Female often darker than male, with much more rufous suffusion, but true rufous or chestnut morph uncommon. Juvenile apparently much like adult in coloration, although often with less contrasting dark markings and with softer-textured plumage. Race *phalaenoides*

smaller, pale and delicately marked, with rufous-morph female commoner than in other races but connected to greyer birds by intermediates; *brachypterus* medium-sized, tends to look rather plainer and perhaps greyer, with no rufous-morph female known. **VOICE.** Calls frequently, especially in breeding season. Song is soft, rather unobtrusive, low-pitched "oom-oom-oom...", typically repeated 10–50 times in successive bursts. Has numerous other calls, and sometimes gives mechanical bill-snaps when threatened.

Habitat. Requires trees or shrubs in which to roost and nest, and perches from which it can hunt in open places, so occurs in most types of country with trees or scrub, including *Eucalyptus* forest and woodland, mulga, trees along watercourses, mallee, coastal scrub, tree-lined roadsides in farmland, city parks and large gardens with trees. Avoids treeless semi-desert and usually the interior of rainforest, although it readily colonizes edges of roadways in rainforest areas.

Food and Feeding. Diet consists mainly of large insects and other terrestrial invertebrates (scorpions, spiders, centipedes); also takes frogs, and occasionally earthworms, snails, slugs, crustaceans

(Decapoda), millipedes, lizards, small birds and small mammals. Typically hunts by sallying from exposed perch, such as an open branch or fence post adjacent to open ground, from which it glides to capture moving prey from the ground or, less often, from branches; often feeds from roadsides, resulting in many birds being killed by traffic. Large or tough prey items are beaten against the perch before being swallowed.

Breeding. Season apparently similar throughout range, mostly Aug-Dec, with peak of laying Sept-Oct. Normally single-brooded; reports of second brood unconfirmed. Nest a coarse, loose and often flimsy, shallow, almost flat platform of criss-crossed thin sticks and twigs, placed on fork of tree, less often on old nest of another bird or on epiphyte, generally 3-10 m (2-20) above ground. Clutch 1-3 eggs, usually 2, rarely up to 5; incubation 28-32 days, by male during day, but female thought to incubate at night; parents feed each other at nest at night; nestling has first down white, second down grey with white flecking and barring and paler underparts; young brooded and fed by both parents; fledging 25-35 days; fledged young fed by parents for 1-2 weeks after leaving nest, and may remain with them for several months longer.

Movements. Adults appear to be sedentary throughout year on their territories; seasonal movements suggested by some authors, but these are unconfirmed and seem unlikely. Extent of dispersal of young birds unknown.

Status and Conservation. Not globally threatened. Remains common over much of Australia, though has declined in some areas, e.g. S Mt Lofty Ras, SE South Australia and Wheatbelt of Western

Australia. A successful colonist of farmland and many built-up areas; often sighted in urban parks and gardens, and in trees lining streets; adversely affected by wholesale extraction of trees to make way for agriculture, but may benefit from partial clearance of dense forest. Evidently capable of withstanding considerable mortality from road traffic, as well as losses due to predation from introduced cats and foxes; however, numbers killed by traffic in N Sydney have dropped notably since early 1970's, possibly reflecting population decline; other man-related negative factors on record include pesticide poisoning, nest disturbance, shooting of birds by vandals, and death caused by birds flying into wire fences. Frequently kept in zoos and bird parks.

Bibliography. Anon. (1995b), Barker & Vestjens (1989), Beruldsen (1980), Blakers *et al.* (1984), Carter *et al.* (1985), Coleman (1946a, 1946b), Condon (1975), Corben & Roberts (1993), Davis & Beehler (1993), Deignan (1951), Disher *et al.* (1995), Dove (1928), Fish (1996), Fleay (1925, 1936, 1979), Ford (1986), Gerrits (1956), Goudswaard (1983), Higgins (1999), Hollands (1991), Holmes (1981), Irby (1927), Kingston (1980), Kutt (1994), Lasiewski & Bartholomew (1966), Lindholm (1988), Lindsey (1992), Lord (1956), Macdonald (1988), Mackay (1976), Mathews (1927), McAllan & Bruce (1989), McCulloch (1975), McNab & Bonaccorso (1995), Mees (1961), Milledge & Clancy (1982), O'Brien (1990), Pizzey & Doyle (1998), Ragless (1955, 1957), Rason (1986), Roberts & Ingram (1978), Rose (1973a, 1976), Rose & Eldridge (1997), Rutgers & Norris (1972), Schodde & Mason (1981), Schodde & Tidemann (1986), Schönwetter (1964), Serventy (1936), Serventy & Whittell (1962), Simpson & Day (1998), Storr (1984), Strahan (1994), Stresemann & Stresemann (1966), Tarr (1985), Thomas (1957), Trounson & Trounson (1987), Vestjens (1973).

intermediate morph

inches 4

mottled morph

chestnut morph

dark morph

chestnut morph

brown-and-buff
morph

black-and-white
morph

ssp mixtus

ssp *javensis*ssp *affinis**ssp continentalis*

poliolophus

Subfamily BATRACHOSTOMINAE

Genus *BATRACHOSTOMUS* Gould, 1838

4. Large Frogmouth

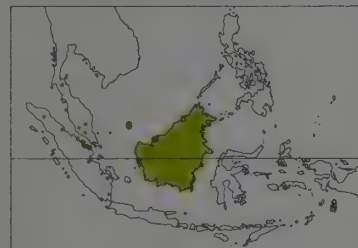
Batrachostomus auritus

French: Podarge oreillard **German:** Riesenfroschmaul **Spanish:** Podargo Orejudo

Taxonomy. *Podargus Auritus* J. E. Gray, 1829, no locality = Sumatra.

Forms a superspecies with the Bornean montane endemic *B. harterti*. Monotypic.

Distribution. Scattered localities in Peninsular Thailand (Nakhon Si Thammarat), Malaysia and Sumatra to Borneo and nearby N Natuna Is and Labuan I.



Descriptive notes. 40-43 cm; c. 206 g. Largest of the Asian frogmouths, although *B. harterti* not much smaller. Adult chestnut to light brown above, with pale bars on scapulars and blackish-edged white or buffy-white spots on wing-coverts; underparts rufous-brown, often with some buff to white spots. No obvious sexual dichromatism. Juvenile apparently differs from adult in having upperparts mainly grey-brown with fine vermiculation of pale buff, and underparts light grey-brown with rufous tinge, paler on belly. Voice. Poorly known; variously described as a loud wheezy call, and as a deep, hollow-sounding tremolo which may

be repeated up to 8 times; also, a repeated rippling "coerr".

Habitat. Lowland rainforest, but recorded from secondary forest as well as undisturbed primary forest; also forest in swamps and on alluvial soils.

Food and Feeding. Diet includes cicadas and grasshoppers. Apparently feeds by sallying to catch insects on the ground or from branches.

Breeding. Season unrecorded. Nest a rather small but thick, circular pad of fine down firmly attached to a slender branch of a shrub or sapling; one was 1-3 m above the ground. Clutch apparently 1 egg; incubation and fledging periods, and roles of sexes in each, unknown; nestling apparently has white down.

Movements. Appears to be sedentary.

Status and Conservation. Not globally threatened. Data-deficient. Extremely rare in Thailand, where possibly only one definite record exists. Rare in Malaysia, but still recorded in areas of fragmented forest around Kuala Lumpur and nearby parts; recent records in three different parts of Taman Negara National Park. Rather few records from Sumatra, where species might be threatened; however, report from Gunung Leuser National Park in 1988, and new provincial records from Riau (a bird mist-netted in 1991) and Lampung (several records from Way Kambas National Park in 1994 and 1995), suggest that it may be more widespread than previously suspected. Seems to be very uncommon in Borneo, where only local in occurrence; recorded in Gunung Mulu National Park, Sarawak, and in Danum Valley Conservation Area, Sabah. In general, apparently an uncommon or rare bird that is almost certainly declining owing to destruction of its lowland-forest habitat, but it is an elusive and little-known species.

Bibliography. Andrew (1992), van Balen (1968), Chasen (1939), Collar *et al.* (1994), Danielsen & Heegaard (1995), Holmes (1996, 1997), Lekagul & Round (1991), MacKinnon & Philipps (1993), Mann (1987), van Marle & Voous (1988), Marshall (1978), Medway & Wells (1976), Nash, A.D. & Nash (1985), Nash, S.V. & Nash (1985, 1988), Parrott & Andrew (1996), Round (1988), Sheldrake (1916), Smythies (1957, 1981), Steinbacher (1950), Stresemann (1937), Stresemann & Stresemann (1966), Wells, D.R. (1985, 1990, 1999).

5. Dulit Frogmouth

Batrachostomus harterti

French: Podarge de Hartert **German:** Hartertfroschmaul **Spanish:** Podargo del Dulit

Taxonomy. *Batrachostomus harterti* Sharpe, 1892, Mount Dulit, c. 700 m [2000 feet], north Borneo. Forms a superspecies with the more widespread, lowland *B. auritus*; both occur at Mt Dulit, with *B. auritus* recorded only at lower elevations; reports of specimens intermediate between the two are apparently erroneous. Monotypic.

Distribution. Mountains of N & C Borneo: known from Mt Dulit, Usun Apau Plateau, Kelabit Uplands (all Sarawak) and Mt Liang Kubung (Kalimantan).



Descriptive notes. 34-37 cm. Coloration very similar to that of the darkest individuals of *B. auritus*, from which it is reliably distinguished only by slightly smaller size (wing 220-229 mm, against 248-278 mm in *B. auritus*). Sexes much alike. Juvenile plumage unknown. Voice. Not described.

Habitat. Apparently lives in forest at sub-montane levels; reliable records at 600-1230 m, reports from lower elevations presumed to be errors.

Food and Feeding. No information.

Breeding. No information.

Movements. No information; presumably sedentary, like congeners.

Status and Conservation. Not globally threatened. Data-deficient. Restricted-range species; present in Bornean Mountains EBA. Apparently known only from seven skins (six from Sarawak and one

from Kalimantan), with no information on its status, past or present. Potentially at risk from deforestation or from collection of specimens. Species clearly in urgent need of intensive study to determine, among other things, its ecology, biology and population levels.

Bibliography. Andrew (1992), Collar & Andrew (1988), Collar *et al.* (1994), MacKinnon & Philipps (1993), Marshall (1978), Sharpe (1892a, 1892b), Smythies (1957, 1981), Stattersfield *et al.* (1998), Stresemann (1937), Stresemann & Stresemann (1966), Sujatnika *et al.* (1995), Warren (1966), Wells (1985).

6. Philippine Frogmouth

Batrachostomus septimus

French: Podarge des Philippines **German:** Philippinenfroschmaul **Spanish:** Podargo Filipino
Other common names: Menage's/Small-billed/Tweeddale's Frogmouth

Taxonomy. *Batrachostomus septimus* Tweeddale, 1877, Pasananca, near Zamboanga, Mindanao, Philippines.

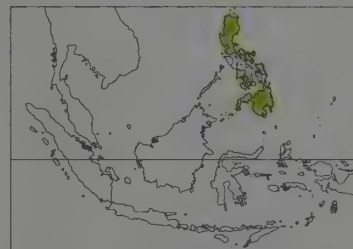
Three subspecies recognized.

Subspecies and Distribution.

B. s. microrhynchus Ogilvie-Grant, 1895 - Luzon and Catanduanes.

B. s. menagei Bourns & Worcester, 1894 - Panay and Negros.

B. s. septimus Tweeddale, 1877 - Bohol, Leyte, Samar, Mindanao and Basilan.



Descriptive notes. c. 25 cm; 75-96.5 g (*septimus*). Nominative form occurs in two colour morphs, connected by intermediates. Adult male has whitish collar across mantle, bold white spots on wing-coverts and much white or pale buff on scapulars; chestnut morph has upperparts mainly rufous-chestnut and ground colour of most of underparts deep rufous; mottled morph has upperparts and underparts mainly light brown with intricate barring of buff and blackish. Distinct from all other *Batrachostomus* in being medium-sized, with relatively short tail. Polymorphic variation formerly misinterpreted as sexual dichromatism; in fact,

female of both morphs differs from male in having narrower white collar across mantle, less white on wing-coverts and no white or pale buff on scapulars. Juvenile undescribed. Races differ mainly in size, with northernmost populations (*microrhynchus*) markedly smaller than nominate, but the two known skins of *menagei* are intermediate in size and come from geographically intervening islands; too few specimens to be sure of occurrence of morphs in both sexes of *menagei* and *microrhynchus*, although both morphs do at least occur in latter race. Voice. Territorial song of female is a single falling note; call of male a faint trill.

Habitat. Forest and near forest edge, from the lowlands to c. 2500 m.

Food and Feeding. No information available.

Breeding. Season Apr-Jun/Jul. Nest described as a small cup of vegetation, placed on tree branch; three reports all refer to nests with single egg; no further information available.

Movements. Presumably sedentary.

Status and Conservation. Not globally threatened. Described as an uncommon species, so some populations are likely to be at risk in view of the extensive deforestation taking place throughout most of the Philippines. Research and survey work required.

Bibliography. Brooks *et al.* (1996), Danielsen *et al.* (1994), Delacour & Mayr (1946), Dickinson *et al.* (1991), Evans, Dutton & Brooks (1993), Gonzales (1983), Goodman & Gonzales (1990), Hachisuka (1930, 1934), Heaney & Regalado (1998), Marshall (1978), McGregor (1904), duPont (1971), Rabor (1938a), Rand & Rabor (1960), Schönwetter (1964), Steinbacher (1949), Stresemann (1937), Whitehead (1899).

7. Gould's Frogmouth

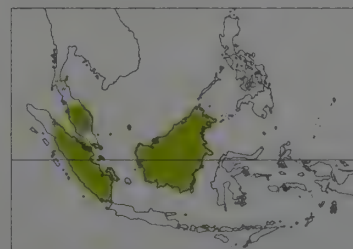
Batrachostomus stellatus

French: Podarge étoilé **German:** Schuppenfroschmaul **Spanish:** Podargo Estrellado

Taxonomy. *Podargus Stellatus* Gould, 1837, Java; error = Malacca.

Apparently a rather isolated species in the genus, differing from other small *Batrachostomus* in lacking sexual dichromatism and in pattern of underpart feathers. Although recognition of Bornean population as a separate race (*parvulus*) is sometimes suggested, geographical variation of species is slight at most. Monotypic.

Distribution. C peninsular Thailand (S from Surat Thani) through peninsular Malaysia (S to Negeri Sembilan) to Sumatra, then E through Riau (Bintan) and Lingga (Lingga) Archipelagos and Bangka to Borneo and Natuna Besar I.



Descriptive notes. 21-25 cm; 47-48.5 g. Occurs in two colour morphs. Adult has narrow whitish collar across mantle, bold whitish spots on wing-coverts and white or greyish-white spots on scapulars, the underparts with oval-shaped buffish spots; chestnut morph has ground colour of upperparts mainly chestnut, that of scarcer dark morph darker, almost blackish-chestnut. Sexes similar (in most but not all of the literature, polymorphic variation in this species misinterpreted as sexual dichromatism). Juvenile also dimorphic, chestnut morph having dull rufous-chestnut upperparts with narrow, ill-defined darker barring, dark morph similar but darker overall, and both plainer and less spotted. Voice. Male's song is a phrase of 2 units, the second higher than the first and connected to it by a brief tremolo. Territorial song of female apparently not described.

Habitat. Rainforest; reported to live in the lower storey and to prefer dense forest; one nest was found in secondary forest. Occurs mainly in the lowlands, up to 500 m; one record at c. 920 m in Borneo.

Food and Feeding. Diet known to include Orthoptera, and also moths and beetles. No further information available.

Breeding. Season poorly known; young in peninsular Malaysia in Jun and Aug; an oviduct egg in Borneo at end of Apr. Few nests described, in all cases a small, neat pad with shallow cup placed on top of thin horizontal branches; one was c. 1.3 m above ground. One clutch contained 1 egg; nestling apparently has white down; incubation and fledging periods, and roles of each sex in caring for eggs and young, unknown.

Movements. Apparently sedentary.

Status and Conservation. Not globally threatened. Although a relatively wide-ranging species, it is doubtless at risk in some areas owing to destruction of lowland rainforest; in Thailand, such loss of habitat has led to its now being regarded as a nationally threatened species. In Sumatra, the only recent reports are from Way Kambas National Park, where species recorded in 1984, 1985 and 1991.

Bibliography. Andrew (1992), Chasen (1931, 1939), Holmes (1996), Lekagul & Round (1991), MacKinnon & Philipps (1993), van Marle & Voous (1988), Marshall (1978), Mayr (1938), Medway & Wells (1963, 1976), Mees (1986), Parrott & Andrew (1996), Riley (1938), Round (1988), Schönwetter (1964), Smythies (1957, 1981), Steinbacher (1949), Stresemann (1937), Stresemann & Stresemann (1966), Voous (1961), Wells, D.R. (1985, 1990, 1999).

8. Sri Lanka Frogmouth

Batrachostomus moniliger

French: Podarge de Ceylan **German:** Ceylonfroschmaul **Spanish:** Podargo de Ceilán
Other common names: Ceylon/Ceylonese/Sinhalese Frogmouth

Taxonomy. *Batrachostomus moniliger* Blyth, 1849, Sri Lanka.

Resembles *B. hodgsoni* in coloration and pattern, and the two species replace each other geographically, but differences in the facial bristles, clutch size, egg size and adult plumage markings imply that they are probably too dissimilar to be regarded as forming a superspecies. Species name sometimes misspelt *monileger*. Monotypic.

Distribution. S India, in high-rainfall areas of Western Ghats from N Kanara district (Karnataka) S to Trivandrum district (Kerala); and Sri Lanka, except in dry N & SE regions.



Descriptive notes. 22–23 cm. A small, sexually dichromatic species, with adult coloration and pattern almost constant for each sex. Male brownish-grey with black and white vermiculations, narrow whitish collar across upper mantle, and white spots on scapulars, wing-coverts, belly and irregularly across breast. Differs from *B. hodgsoni* in greyer coloration and less heavily marked underparts. Female rufous or rufous-brown and more uniform, with less distinct collar and fewer spots. Juvenile female apparently has coloration much as adult female, but with softer-textured plumage; juvenile male also appears to be similar.

but few immature specimens available. Voice. Mainly a soft, rapid series of "koo-roo, koo-roo, koo-roo" units, though various other vocalizations also reported.

Habitat. Woodland and forest; often found in dense vegetation such as bamboo thickets or in second growth, remaining mainly in the understorey. Occurs from sea-level up to 1200 m, possibly to 1800 m.

Food and Feeding. Little known. Recorded prey includes grasshoppers and a beetle. Catches insect prey on the ground or on branches.

Breeding. Season apparently long, in S India chiefly Jan–Apr, occasionally Jun–Sept; in Sri Lanka mainly Feb–Mar, occasionally Sept. Nest is a small circular pad composed mainly of the birds' own down, placed on horizontal branch or in fork of small tree 2–6 m above ground. Clutch 1 egg; incubation by both sexes, by male during the day; nestling has first down white, second down rufous-buff, paler beneath, with narrow dark barring; incubation and fledging periods and care of young undescribed.

Movements. Apparently sedentary.

Status and Conservation. Not globally threatened. Currently considered Near-threatened. Recent surveys suggest that it is local and uncommon in S India, but not endangered, although destruction of wet forest in Western Ghats continues. Widespread in Sri Lanka, but apparently scarce or rare; frequently recorded in Sinharaja Forest Reserve. Possibly under-recorded throughout range.

Bibliography. Ali & Ripley (1983), Baker (1934a, 1934b), Borges (1986), Daniels (1997), Gaston & Zacharias (1996), Grimmer et al. (1998), Henry (1998), Hoffmann (1998), Kannan (1993a, 1994b, 1998), Lamsfuss (1998), Legge (1983), Marshall (1978), Phillips, W.W.A. (1947, 1978, 1979), Ripley (1982), Schönwetter (1964), Serventy (1936), Steinbacher (1949), Stresemann (1937), Stresemann & Stresemann (1966), Sugathan (1981), Sugathan & Varghese (1996), Vijayan (1978).

9. Hodgson's Frogmouth

Batrachostomus hodgsoni

French: Podarge de Hodgson **German:** Langschwanz-Froschmaul **Spanish:** Podargo Colilargo

Taxonomy. *Otothrix hodgsoni* G. R. Gray, 1859, northern India = Darjeeling, Sikkim.

Resembles *B. moniliger* in coloration and pattern, and the two species replace each other geographically, but differences in the facial bristles, clutch size, egg size and adult plumage markings suggest that they are probably too dissimilar to be regarded as forming a superspecies. Sometimes treated as a race of *B. javensis*, but differences in bill size and structure, development of facial bristles, relative tail length and vocalizations, and also perhaps in bare-part colours (bill said to be darker), too great for them to be considered even as forming a superspecies. Populations from S parts of Myanmar to Indochina often separated racially as *indochinae*; they average smaller and shorter-tailed, but measurements overlap with those from India. Manipur birds ("*ruphandi*") are apparently inseparable from other Indian populations. Monotypic.

Distribution. Hills and lower mountains of NE India (Sikkim, Assam and Arunachal Pradesh S to Manipur and Tripura) and SE Bangladesh through N, W & E Myanmar to SW China (SW Yunnan), NW Thailand, NW & S Laos and C Vietnam (Annam).

Descriptive notes. 22–27 cm; 51 g. A small *Batrachostomus* with well-marked sexual dichromatism, but little variation in coloration of adult of either sex. Male rufous-brown above, heavily marked with black, with white spots on scapulars and upper mantle, where may form collar; black, white



and lower montane slopes, at 300–1900 m elevation.

Food and Feeding. Diet consists of moths, beetles and other large insects. Recent accounts suggest that food is hawked in air or taken on ground or from branches; older accounts of feeding behaviour probably unreliable.

Breeding. Season Apr–Jul in NE Indian region; laying in Annam in late Feb or early Mar. Nest is a small, neat pad composed mainly of the birds' down, placed on bare or nearly bare horizontal branch c. 1.5–5 m above ground. Clutch usually 2 eggs, sometimes 1; male incubates during daytime, female in evening twilight and for 1–2 hours before dawn; incubation and fledging periods and care of young undescribed; nestling has (second?) down bright rufous or dull buff with darker barring.

Movements. Apparently sedentary.

Status and Conservation. Not globally threatened. Apparently rare in many parts of E Himalayas and foothills, and certainly rare in Bangladesh; formerly rare in much of Myanmar, except in Chin Hills; uncommon in Thailand, but not regarded as a threatened species there. Current status poorly known throughout range.

Bibliography. Ali & Ripley (1983), Ali et al. (1996), Baker (1934b), Delacour & Greenway (1940), Dickinson (1970), Evans & Timmins (1998), Grimmer et al. (1998), Harvey (1990), Lekagul & Round (1991), Marshall (1978), Pilo et al. (1996), Ripley (1982), Round (1988), Schönwetter (1964), Serventy (1936), Smythies (1944, 1986), Stresemann (1937), Thewlis et al. (1996), Wang Sung (1998), Zhao Zhengjie (1995).

10. Short-tailed Frogmouth

Batrachostomus poliophus

French: Podarge à tête grise **German:** Graukopf-Froschmaul **Spanish:** Podargo Colicorto
Other common names: Pale-headed Frogmouth; Bornean/Sharpe's Frogmouth (*mixtus*)

Taxonomy. *Batrachostomus poliophus* Hartert, 1892, Padang, West Sumatra.

Race *mixtus* has often been regarded as a separate species, an arrangement apparently initiated in 1937 by cautious uncertainty expressed regarding the characters of the then unknown male of the nominate form. Subsequent to the latter being described in 1938, the two forms seem not to differ greatly in coloration of either sex, and the extreme measurements of each closely approach those of the other, so that their treatment as races of the same species would seem more appropriate; possible differences in vocalizations, however, require investigation. Two subspecies recognized.

Subspecies and Distribution.

B. p. poliophus Hartert, 1892 – Sumatra.

B. p. mixtus Sharpe, 1892 – Borneo.



Descriptive notes. 20–22 cm. A sexually dichromatic species, with no apparent polymorphic variation in coloration; sexes confused in early accounts. Male dull dark rufescent-brown with buffish-white collar across upper mantle, and bold white spots on scapulars and wing-coverts; breast with white scallop-shaped markings, flanks and belly whitish with brownish edges to feathers. Differs from other small, sexually dichromatic *Batrachostomus* in combination of relatively short tail and details of coloration (as well as sub-montane distribution). Female brighter, deep rufous to chestnut, with reduced white

spotting, and often narrower collar. Juvenile plumage unknown. Voice. Only very recently described, for both races. Song (perhaps call) said to be a fairly loud undulating whistle, rising in pitch, followed by 5–7 descending liquid notes. Song (or call) of *mixtus* described as a whistled "weeow" repeated at c. 3-second intervals, each note sometimes wavering towards end; also high-pitched "chiok, chiok, chiok" series, perched or in flight, possibly as alarm.

Habitat. Sub-montane primary forest and mixed pine forest. Generally tends to occur at somewhat higher altitudes than other *Batrachostomus*: recorded at 600–1400 m in Sumatra; in Borneo mostly 610–1700 m, occasionally to 2540 m.

Food and Feeding. Gut contents of specimens examined included remains of small beetles and small Orthoptera.

Breeding. Few data. Known mainly from a single nest found in Sumatra in Jun 1933: a small pad with shallow cup, built mainly of down from birds' underparts, placed c. 5 m above ground at fork of inclined branch of a sapling; it held 1 partly incubated egg, and the male incubated during the daytime.

Movements. No information, but presumably sedentary like its congeners.

Status and Conservation. Not globally threatened. Both races listed as Data-deficient. Restricted-range species: present in Sumatra and Peninsular Malaysia EBA and Bornean Mountains EBA. Reported as uncommon in Sumatra, though several records in 1990's from N and W. Probably not common in Borneo, but occurs in Mt Kinabalu and (almost certainly) Gunung Mulu National Parks; recent record from S Kalimantan probably refers to present species. In both Sumatra and Borneo, species appears to have a relatively small range, in parts of which the forest is being destroyed; specimens are few in collections. The species' voice, however, is still poorly known, having only recently been described, so that its true status is difficult to judge.

Bibliography. Andrew (1992), Bartels (1938), Collar et al. (1994), Davison (1997a), Holmes (1996, 1997), Hoogerwerf (1962), Inskipp et al. (1996), MacKinnon & Philipps (1993), van Marle & Voous (1988), Marshall (1978), Philipps (1981/82), Schönwetter (1964), Sharpe (1892c), Smythies (1957, 1981), Stattersfield et al. (1998), Steinbacher (1949, 1950), Stresemann (1937, 1938b), Sujatnika et al. (1995), Vowles & Vowles (1984), Wells (1985).

11. Horsfield's Frogmouth

Batrachostomus javensis

French: Podarge de Java **German:** Javafroschmaul **Spanish:** Podargo de Java
Other common names: Javan Frogmouth; Blyth's Frogmouth (*affinis*); Indochinese Frogmouth (*continentalis*); Palawan Frogmouth ("chasei")

Taxonomy. *Podargus Javensis* Horsfield, 1821, Java.

Much confusion over species-limits with regard to this and its close allies. Formerly considered conspecific with *B. cornutus* by some, but a combined study of vocalizations and museum specimens in 1978 confirmed earlier suggestions that it should be regarded as a distinct species. Race *affinis* sometimes considered a distinct species. Sometimes treated as conspecific with *B. hodgsoni*, but differences in bill size and structure, development of facial bristles, relative tail length and vocalizations, and also perhaps in bare-part colours (bill said to be often more straw-coloured), too great for them to be considered even as forming a superspecies. Race *continentalis* is apparently connected to *affinis* by an intermediate population around Khao I Phrom in C peninsular Thailand. Birds from Palawan, Culion I and Banggi I often separated as race *chasei*, but appear inseparable from *affinis*; recent claim of a new species (*B. pygmaeus*) from Palawan (Basuanga I) seems unconvincing, the single specimen on which description is based being little different from local "chasei" (= *affinis*). Three subspecies recognized.

Subspecies and Distribution.

B. j. continentalis Stresemann, 1937 - SE Myanmar (S Tenasserim) and N, W & S Thailand (S to Nakhon Si Thammarat); also S Laos and C Vietnam (Annam).

B. j. affinis Blyth, 1847 - SE peninsular Thailand S to Sumatra and Riau Archipelago, then E through Borneo and Banggi I (off N Borneo) to W Philippines (Palawan, Culion I).

B. j. javensis (Horsfield, 1821) - Java.

Descriptive notes. 19-25 cm; mean 46-47 g. A small, sexually dichromatic *Batrachostomus* with no polymorphism in plumage coloration. Male brown above, speckled white and with distinct black spots; whitish supercilium, whitish collar across upper mantle, and much white on scapulars; spotted cinnamon, buff and white below, belly and flanks brown-barred whitish. Female notably brighter and plainer, with less white. Juvenile little known, but said to be pale rufous with faint barring and speckling above; a juvenile male of race *affinis* had plumage softer-textured than adult, coloration much more rufous in tone than adult male, with



more prominent dark barring, and underparts more like adult female. Races differ mainly in tone of coloration, or details of colour pattern, or both. Voice. Territorial song of female a frenzied, descending series of 3-5 units, sounding like maniacal laughter; male gives a plaintive whistle.

Habitat. Mainly lowland evergreen forest, preferring dense rainforest, in which it lives mostly in the understorey. Also reported from tree-rich scrub in Java, and occurs locally in mixed deciduous forest in Thailand, including that on limestone crags; recorded in mangroves in S Sumatra; some accounts list second growth among its habitats. Occurs from sea-level up to 1600 m, but to 1700 m in W & C Java and to 2150 m in E Java.

Food and Feeding. Diet consists mainly of insects, particularly beetles and grasshoppers; other records from gut contents include moths, caterpillars, earwigs, cockroaches, termites and a snail. Scant information implies that prey is captured mainly by fluttering at leaves and trunks, with some perhaps taken from ground or in flight.

Breeding. Few data on season: 2 nests with eggs in Malaysia in Feb and Mar, and 1 with nestlings in Palawan in Jul; possibly Jan-Apr in Borneo, and Feb to mid-Jun in Java. Nest is a small rounded pad with shallow cup, built mainly from the birds' own down, placed on branch of small sapling or a *Saccharum* cane. Clutch 1-2 eggs; a male has been recorded incubating during the daytime; incubation and fledging periods and care of young undescribed.

Movements. Apparently sedentary.

Status and Conservation. Not globally threatened. Currently considered Near-threatened; this assessment probably results from taxonomic confusion, since only the Javan nominate subspecies is scarce, although local populations in many other regions are at risk from deforestation. Status uncertain in Sumatra, but several recent records from Way Kambas National Park. On Palawan, regularly recorded in St Pauls National Park. Calls thought to refer to present species heard relatively commonly in Laos during fieldwork in mid-1990's. Despite its relatively wide distribution, species remains poorly known, and may well be under-recorded throughout much of range.

Bibliography. Andrew (1992), Bartels (1938), Bernstein (1860), Chasen (1931, 1939), Delacour & Mayr (1946), Dickinson *et al.* (1991), Duckworth (1996), Evans & Timmins (1998), Hachisuka (1934), Holmes (1996, 1997), Holmes & Burton (1987), Hoogerwerf (1962), Hoogstraal (1951), Inskipp *et al.* (1996), Lekagul & Round (1991), MacKinnon (1988), MacKinnon & Philipps (1993), Mann (1989), van Marle & Voous (1988), Marshall (1978), McGregor (1909-1910), Medway & Nisbet (1965), Medway & Wells (1976), Mees (1986), Mitsch (1987), Nash & Nash (1988), Parrott & Andrew (1996), duPont (1971), Riley (1938), Round (1988), Schönwetter (1964), Smythies (1957, 1981, 1986), Steinbacher (1949), Stresemann (1937), Thewlis, Duckworth *et al.* (1996), Thewlis, Timmins *et al.* (1998), Verheugt *et al.* (1993), Wells (1985, 1999), Wells & Medway (1976).

12. Sunda Frogmouth

Batrachostomus cornutus

French: Podarge cornu **German:** Sundafrschmaul **Spanish:** Podargo Cornudo
Other common names: Horned/Long-tailed Frogmouth

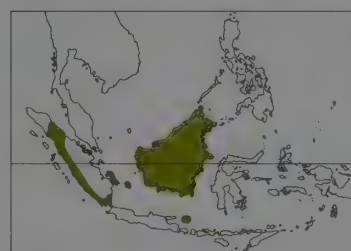
Taxonomy. *Podargus cornutus* Temminck, 1822, Bengkulu, Sumatra.

Formerly considered conspecific with *B. javensis* by some, but a combined study of vocalizations and museum specimens in 1978 confirmed earlier ideas that the two should be regarded as separate species. Recent suggestion that a population of small *Batrachostomus* in Palawan ("chasei") may be a race of present species appears to be without foundation, since *chasei* is best regarded as a synonym of *B. javensis affinis*. Two subspecies recognized.

Subspecies and Distribution.

B. c. cornutus (Temminck, 1822) - Sumatra, Bangka and Belitung to Borneo and Banggi I (off N Borneo).

B. c. longicaudatus Hoogerwerf, 1962 - Kangean Is (NE of Java).



Descriptive notes. 23-28 cm. Plumage coloration very variable, and much confusion in the literature over how much of the variation is attributable to sexual dichromatism and how much to polymorphism. Adult male has broad pale supercilium, pale collar across upper mantle, and prominent whitish oval spots on scapulars; underparts mottled, belly and flanks paler with dark spots and bars. Occurs as two colour morphs, with intermediates: black-and-white morph has upperparts blackish, finely freckled and vermiculated with whitish to pale buff; brown-and-buff morph similar in general pattern, but with the blackish areas replaced

by brown and the whitish areas replaced by pale buff. Adult female varies from rather plain, with much deep rufous on upperparts and rufous on underparts, to so heavily freckled as to resemble brown-and-buff morph of male. The only juvenile specimen seen, a female, had soft-textured plumage and coloration closest to that of most rufous variants of adult female, but with lighter upperparts and underparts. Race *longicaudatus* averages longer-tailed and thinner-billed, with less contrast in plumage. Voice. Territorial song, presumably of female, a descending series of "qwa" units, like "caw" of Large-billed Crow (*Corvus macrorhynchos*).

Habitat. Differs from congeners in occurring mainly in secondary forest or at forest edge; also reported in low riverside bushes and occasionally in mangroves and in village gardens; reported occurrence in (tobacco and) rubber plantations, in Sumatra, not definitely attributable to present species. Mostly found in lowlands, but ascends to 1000 m.

Food and Feeding. One stomach contained beetle remains. No further information available.

Breeding. Poorly known. Only data on season from Sumatra: an egg in Jun and a nestling in early May. Nest is a small rounded structure with shallow cup, built mainly of down, moss and small bark fragments, placed on horizontal branch. Clutch 1 egg; incubation and fledging periods, and roles of sexes in caring for eggs and young, undescribed.

Movements. Apparently sedentary.

Status and Conservation. Not globally threatened. Little recent information on its status, but probably the commonest of the smaller *Batrachostomus* in Borneo; only recent records from Sumatra are several from Way Kambas National Park. The species' preference for second growth suggests that it may be less at risk from loss of habitat than are its sympatric congeners that require primary rainforest.

Bibliography. Andrew (1992), van Balen (1968), Chasen (1937), Coomans de Ruiter (1931, 1935), Hachisuka (1934), Holmes (1996), Hoogerwerf (1962), Inskipp *et al.* (1996), MacKinnon (1988), MacKinnon & Philipps (1993), van Marle & Voous (1988), Marshall (1978), Mees (1986), Parrott & Andrew (1996), Schönwetter (1964), Smythies (1957, 1981), Stresemann (1937), Stresemann & Stresemann (1966), Wells (1985), Wells & Medway (1976).

Class AVES
Order CAPRIMULGIFORMES
Suborder CAPRIMULGI
Family NYCTIBIIDAE (POTOOS)



- Medium-sized nocturnal birds with large head, small body, long wings and tail, and very short legs.
- 21-58 cm.



- Neotropical.
- Forests, mainly humid.
- 1 genus, 7 species, 15 taxa.
- No species threatened; none extinct since 1600.

Systematics

The potoos are endemic to the Neotropics, where they are known from every mainland country except Chile, reaching their greatest diversity in the Amazonian lowlands. They are an ancient lineage and, based on the existence of a European fossil, apparently were once more widespread than at present. The oldest fossil, a single leg bone of the extinct species *Euronyctibius kurochikini*, is from France and is at least 25 million years old, dating from the Upper Eocene to the Upper Oligocene. By that time, the modern tropical caprimulgid families had already evolved. Modern potoo species probably existed well before the Pleistocene, from which period date the only other two fossils known, both identified as the Common Potoo (*Nyctibius griseus*), and both from within its modern distribution.

The family Nyctibiidae is a uniform and undisputedly monophyletic group within the order Caprimulgiformes. Various morphological and behavioural features distinguish potoos from the other families, such as the "toothed" bill, the lack of rectal bristles, and, as compared with most of the other families, the upright perching posture (see Morphological Aspects). The relationship of potoos to the other caprimulgid families, however, is less evident. In their upright posture, they resemble frogmouths (Podargidae) of the Old World, with which they have sometimes been allied, along at times with the Oilbird (Steatornithidae). More often, though, the nightjars (Caprimulgidae) are thought to be potoos' closest relatives. In fact, the earliest potoo species discovered were originally described in the genus *Caprimulgus*. A recent molecular study placed the potoos as sister to a group comprised of the nightjars (including the *Eurostopodus* eared-nightjars) and the owl-nightjars (Aegothelidae). In general, though, biochemical studies have found all the caprimulgid families to be highly genetically differentiated, probably a consequence of their great old age. The result is that the families have numerous unique characteristics, a few characteristics shared by all members of the order, and a seemingly random distribution of traits shared with one or another family that could be due as much to convergence over long periods of time as to genetic relatedness. This makes it difficult to establish with any certainty the relationships among the families.

The seven extant species of potoos all belong to the genus *Nyctibius*. The levels of genetic divergence among these species, however, may be the greatest in any single genus of birds, and are equal to or greater than those typically found among birds in

different genera or even families! This suggests that the species too are very old, once again hindering phylogenetic analyses. It is possible that this genetic differentiation, although not obviously reflected in morphological differences, will be acknowledged in the future by separating the most divergent forms into distinct genera.

Likewise within species, a lack of conspicuous geographical variation in morphology might mask strong genetic differentiation. Within a single subspecies of the Great Potoo (*Nyctibius grandis*), for example, genetic divergence between populations on opposite sides of the Andes is comparable to that among distinct potoo species. Thus, it is conceivable that future study will reveal the presence of unrecognized "cryptic species" of potoos. In Costa Rica, what was previously thought to be a single widespread race, *costaricensis*, of the Common Potoo actually contains two vocal types now recognized as belonging to distinct species, the Northern Potoo (*Nyctibius jamaicensis*) and the Common Potoo. Nevertheless, no consistently diagnostic morphological features have yet been identified to distinguish them (see Voice). On the other hand, in the Long-tailed Potoo (*Nyctibius aethereus*), two races, the nominate and *longicaudatus*, originally described as distinct species based on rather striking size and colour differences, are reported not to differ vocally. In this case, the vocal similarity between the two populations might be just another example of the conserved nature of potoo phenotypes over long periods of time.

Despite the conservative phenotypes, individual variability in potoo plumages is considerable, sometimes as much among individuals within a population as between supposedly distinct subspecies. This, coupled with a general shortage of data, due in large part to the difficulty of studying nocturnal birds, has further hindered progress in recognizing taxonomic limits and phylogenetic relationships. Many new taxa were described based on one or a few specimens and incomplete knowledge of species' distributions. Hence, a somewhat different-looking individual in a new part of a species' known range was interpreted as representing a new taxon, rather than as a previously undocumented variant within the normal range of variation, or as an extreme in a continuum of geographical variation. This is the case for the mainland Middle American subspecies of Northern Potoo, which on further study might prove to grade into one another over a continuous range. Similarly, the great individual colour variation and longitudinal size trends (see Morphological Aspects) in Great Potoos, may render the race *guatemalensis*

undiagnosable by morphology. However, if the Andes prove to be a clear barrier between genetically disparate forms, as already suggested, then the name *guatemalensis* may better be applied to the entire Great Potoo population west of the Andes through Middle America.

Another example of these problems is the currently invalidated subspecies *N. griseus cornutus*, originally described from Paraguay in 1817. As early as the 1920's, A. Wetmore recommended that *cornutus* be synonymized with nominate *griseus* (which itself had been overlooked in the literature for over a century), pointing out that the species' considerable individual variation in plumage colour is an obstacle to proper classification. Wetmore's suggestion was corroborated by subsequent study in Brazil by O. Pinto and colleagues and generally adopted in the Brazilian literature. Without any further evaluation and apparently overlooking Wetmore's work, however, the English-language literature maintained the taxon *cornutus* up to the present, applying the name to all *griseus* south of the River Amazon. A study by L. I. Davis even proposed that *cornutus* be elevated to full species rank based on vocalizations of a single individual in Peru. Even if the subtle distinctions of those songs represent an entire population, rather than simply the individual recorded, it is not clear that the Peruvian population would refer to typical *cornutus*, from Paraguay. Until thorough studies are conducted, *cornutus* can not be considered distinctive on the basis of either voice or morphology.

Molecular evidence suggests that Andean Potoo (*Nyctibius maculosus*) and the lowland White-winged Potoo (*Nyctibius leucopterus*) are most closely related, and that they share a common ancestor with the widespread Common Potoo. The phylogenetic relationship of the other species is not as clear. Based on similarity in vocalizations, one author suggested that the Northern Potoo, long considered conspecific with Common Potoo, is actually closer to the Great Potoo. This rather unlikely hypothesis has not been tested rigorously. The notable vocal similarity between Long-tailed and Andean Potoos could also be interpreted as indicating close relationship, although no such suggestion has been forwarded in the literature, and other evidence seems to argue against this interpretation. Much work remains on the evolutionary history and relationships of potoos.



Though in their characteristic sharply upright perching stance potoos resemble the frogmouths (Podargidae) of South-east Asia and Australasia, they seem to be most closely related to the nightjars (Caprimulgidae), but they have distinctive features of their own, such as a toothed bill with no adjacent bristles. There are complex inter-relationships of size, colour and song-type both within and between some potoo species. Thus, the Common Potoo is now separated from the Northern Potoo (*Nyctibius jamaicensis*), though they can be distinguished only by voice.

[*Nyctibius griseus*,
Costa Rica.
Photo: Michael &
Patricia Fogden]

As recently as 1989, a new population of potoos was discovered in Amazonia. These birds closely resemble the White-winged Potoo, itself known only from two museum specimens collected in the nineteenth century, probably in Brazil's Atlantic rainforest. Research in progress has turned up this Amazonian form in widespread localities throughout the basin. Subtle but consistent differences between the Amazonian and Atlantic forms suggest that the Amazonian birds are distinct, and they will receive their own designation, at least as a separate subspecies. However, considering how in potoos even small phenotypic differences can correspond to enormous genetic divergence, this Amazonian bird might best be considered a new species.

Morphological Aspects

Potoos are strange-looking birds. Structurally, they are very much like large, upright nightjars. Their vertical posture lends them a resemblance to frogmouths, which, however, are stockier and have much heavier bills. They also look remarkably like owls, especially when not in their defensive "freezing" posture (see General Habits). Potoos have a disproportionately big head and long wings and tail, relative to their small body and very short legs. The head is dominated by huge eyes and an enormously wide, frog-like mouth, with the bill so short that it barely projects out of the fluffy face. Despite the large head, the brain is tiny, in the smaller species merely the size of a peanut or of a hummingbird's brain. The potoo body is also deceptively small, as attested by their light weight for their size. In a perched bird, more than half of its length, made up entirely of the wings and tail, extends below the perch. In effect, the potoo as a machine is little more than a flying mouth and eyes. Because potoos are rarely observed in the wild, their behaviour is poorly known, and in many cases the connection between their unusual morphology and its function in their lives is a matter of speculation.

All potoo species share the same general morphology, including a number of distinguishing features. The delicate bill is much like that of nightjars, having a very short culmen and wide gape; however, the cutting edge of the maxilla (upper mandible) has a unique, tooth-like projection positioned well to either side of the tip of the bill, which may have a role in foraging (see Food and Feeding). Unlike the similar-looking nightjars, potoos do not have rictal bristles, that is, bristles at the corners of their mouth. They do, however, have some thin bristles emanating from the loreal region between the eye and nostril. Bristles at the base of the bill are also found in many unrelated bird species, especially those that take large or flying insects by capturing them directly in their bills, such as puffbirds (Bucconidae), some wood-warblers (Parulidae), and most tyrant-flycatchers (Tyrannidae). In general, it is believed that these help in detecting or capturing flying prey, or in protecting the predator's eyes.

Potoo eyes are very large, even relatively larger than in the other caprimulgiforms, and at night they reflect a strong red or orange glow in the beam of a flashlight. Large eyes and widely dilating pupils (the reason they reflect so much light in the dark) are an adaptation to life at night and are found throughout the order Caprimulgiformes, as well as in other nocturnal animals, including frogs and cats. The position of their eyes, bulging upward and outward at the sides of the head, enables potoos to see in most directions without turning. Most potoo species have a bright yellow iris; however, the iris of the Rufous Potoo (*Nyctibius bracteatus*) has a dark wedge in the lower portion, and the Great Potoo's is brown. The upper eyelids of all potoos have two or three small folds along their edge, which create notches or slits. The result is that, even when their eyes are closed, potoos have small "peek-holes", through which they can probably detect motion. This so-called "magic eye" probably helps them maintain their camouflage by permitting them to see during the day without conspicuously opening their enormous eyes.

The feet are small and weak, and are barely used for anything other than perching quietly on branches. Potoos are not known to capture prey with their feet or to walk or even to move much on their perches, and only exceptionally will they land on the ground. The underside of their toes has a thick, fleshy pad,



One of the camouflage classics of the animal world: this Great Potoo seemingly turns itself into the thick broken-off stump of a tree branch, as it passes away the daylight hours in peaceful inactivity. For potoos, the roost-site is typically high in a tree in the shadow of the crown, though, depending on local conditions, a bird may spend the day in the full glare of the sun, even in a quite exposed and conspicuous spot.

[*Nyctibius grandis grandis*, Hato Piñero, central Venezuela. Photo: Robin Chittenden/FLPA]

no doubt an adaptation to their sedentary, perched lifestyle. As in most other caprimulgid families, they lack the unique, comb-like middle claw of nightjars, which is presumably used in preening in that family. Potoos have powder-down patches on the breast and sides and have an oil-gland, both of which are related to preening, although this has rarely been observed in this family.

Potoos' flight is silent and manoeuvrable. In addition to being long, their wings are relatively broad and round-tipped, providing considerable lift for the birds' light weight. Potoos beat their wings stiffly and buoyantly, much like nightjars or enormous butterflies. They often glide on flat wings, the tips held slightly downward, like owls. In direct flight or glides, the long tail is held closed; but on landing or when abruptly changing direction in pursuit of prey, they spread the tail wide open. Broad, fluffy feathers with aftershafts contribute to their noiseless flight.

The differences among potoo species are mostly in size and coloration. The largest, the Great Potoo, at about 500-600 g, is the size of a big owl, whereas the diminutive Rufous Potoo weighs only about 50 g, roughly the size of a large martin. Despite this size range, overall body proportions are similar among the species. The exceptions are the two largest species. Great Potoos are relatively bulky and heavy-bodied, whereas Long-tailed Potoos have disproportionately long tails. Size variation within the widespread species, such as the Great Potoo and the Northern-Common Potoo superspecies, tends to follow Bergmann's Rule, with size increasing with distance from the equator, even within their entirely tropical distribution.

Most species have complex and cryptic plumage patterns of browns and greys, with extensive fine barring, streaking and mottling, much like that found throughout Caprimulgiformes. Typically, they are somewhat paler below than above, with a pale throat and a dark-barred tail. Several species have variably pale secondary coverts, creating a wing patch, which is most developed in the White-winged Potoo. Also, most species have variable densities and distribution of dark blotches on the breast, sometimes giving the impression of a breastband. The Great Potoo is the palest and most variable species; some individuals are nearly white. The exception to the typical potoo plumage pattern is the Rufous Potoo, which is a nearly uniform bright rufous throughout, interrupted only by black-bordered white spots on its body feathers. It is remarkably similar in plumage to the Oilbird

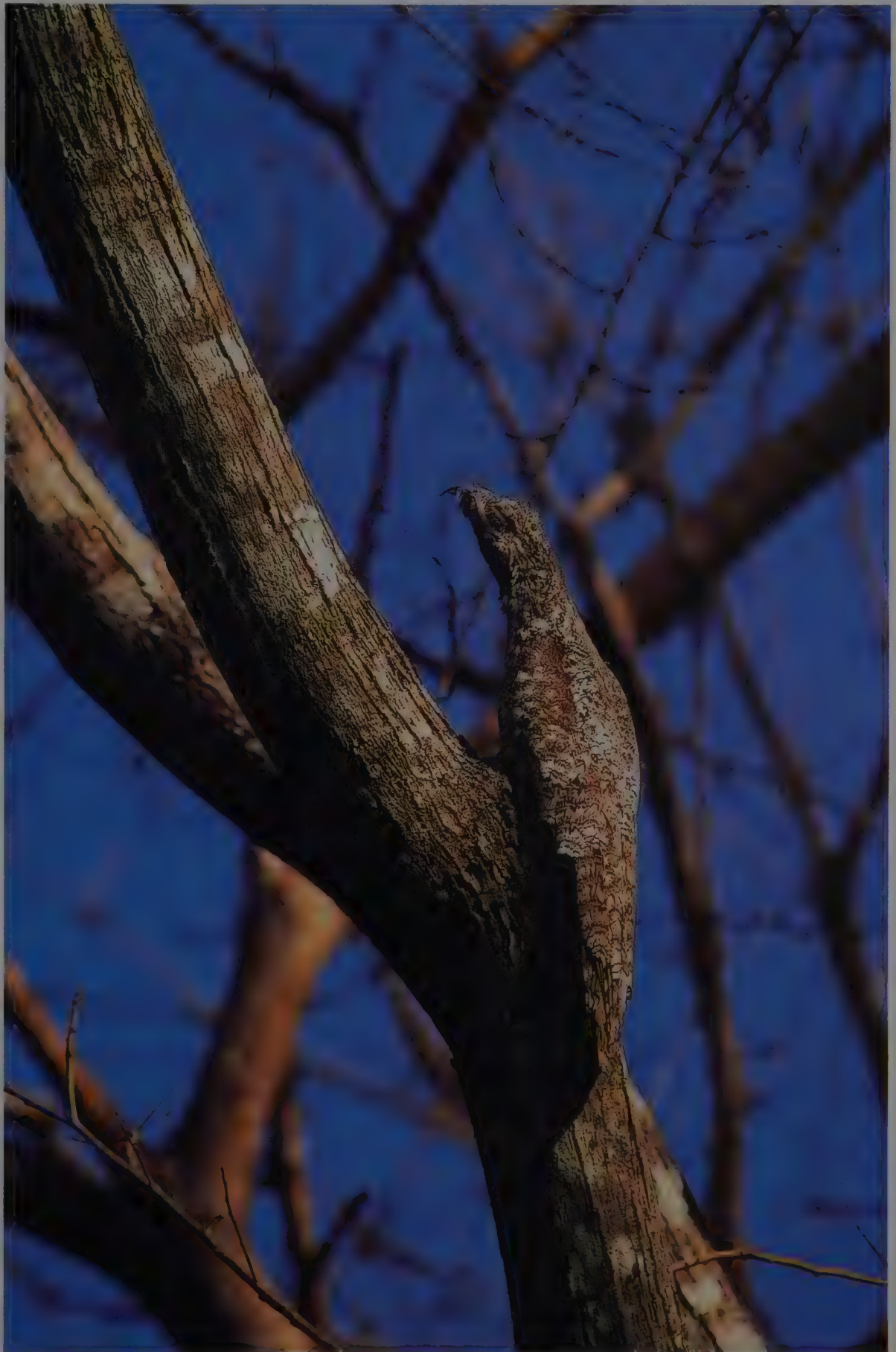
(*Steatornis caripensis*) and to the red colour morph of some nightjars and owlet-nightjars. Reddish tones are found to varying extents in the feathers of the other, predominantly brown and grey species, as well. It has been suggested that potoos have red and grey colour morphs, as in some other caprimulgiforms and owls. However, their considerable intraspecific plumage variability does not seem to fall neatly into distinct colour morphs. Although potoos have no described sexual dimorphism in size or coloration, some of their individual plumage variation may prove to be associated with age or sex.

As might be expected in birds that depend on camouflage for defence, potoo plumage colour appears to be subject to strong natural selection. Coloration within widespread species is often paler in populations in drier environments, such as Caribbean versus mainland Northern Potoos, and so seems to obey Gloger's Rule.

Juvenile plumage is mostly undescribed, but all the species in which the juvenile is known show distinctive juvenile plumages. In several cases they are much paler than the adult form, sometimes nearly pure white. Juvenile Rufous Potoos, by contrast, are darker and browner than adults, with markings more typical of the adults of other potoo species.

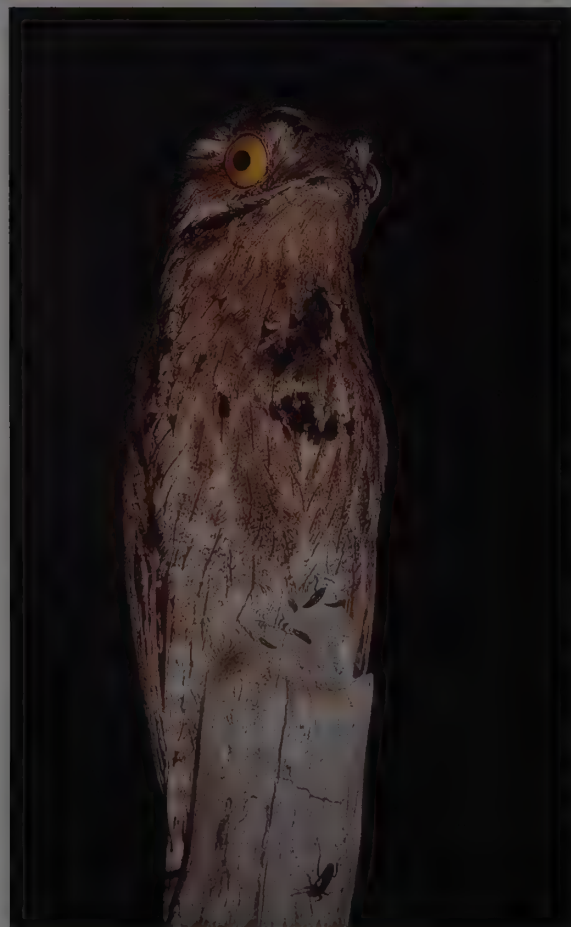
Habitat

Potoos are forest birds, all species occurring in dense humid forest, although some also occur in drier forest or in patches of trees amidst lower vegetation. All five lowland Amazonian species can be found in the same *terra firme* woods, whereas in seasonally flooded *várzea* usually only Common and Great Potoos are found. Long-tailed, White-winged and Rufous Potoos all seem to be patchily distributed throughout Amazonian rainforest. This could be due to subtly differing habitat preferences not yet detected or simply to lack of observations. The Common Potoo is especially flexible in its habitat selection, inhabiting rainforest, dry forests, *cerrado*, mangroves, partially disturbed areas, and tall second growth. Its sister species, the Northern Potoo, is also fairly flexible, occurring in humid and dry forests, as well as plantations. All species are limited to the tropical lowlands, except the Andean Potoo, which occurs in cloudforest along a fairly narrow elevational belt in the Andes.



The perfection of a potoo's camouflage must surely make a major contribution towards keeping it secure from the vast majority of its potential daytime predators, looking as it does like dry, cracked bark with a spattering of lichens. The Great Potoo is more variable in its plumage even than are other members of the family, and some individuals can be almost white; such variation may be linked to the habitats occupied by the different populations, as certainly seems to be the case with the Northern Potoo (*Nyctibius jamaicensis*). When roosting in the full sun, a potoo will sometimes sit with the head turned away from the direction of the sun's rays and the bill held very slightly open, as it relieves itself from heat stress with some surreptitious panting. Otherwise, it is quite normal for the roosting bird to make virtually no other movements for hours on end.

[*Nyctibius grandis grandis*,
Venezuela.
Photo: François Gohier]



Most species occur in the canopy, foraging from exposed perches, especially bare snags, in the tops of tall trees. Because they forage in the open air, several species will venture out along forest edges, sometimes even into pastures, where they will perch on fenceposts. Great, Northern and Common Potoos are the species most regularly found in open habitats at night; however, they are rarely far from forest. The most strictly forest-based species is the Rufous Potoo: it typically stays in the understorey and middle storey of tall rainforest, sometimes less than a metre off the ground, although it too will forage up in the canopy and at the edge of treefall gaps. The Long-tailed Potoo also forages in the shady interior of rainforest, but seems just as at home at edges and even in the open near forest. The White-winged Potoo, on the other hand, stays strictly in the canopy of tall forest, unless at an edge, where it might drop lower accompanying the height of the tallest vegetation.

During the day, potoos typically roost high in trees, but usually in the shadow of the tree crown, along relatively heavy, bare branches where they look like stubs. Potoos have been reported roosting atop telephone poles, and the Great Potoo is regularly seen during the day on exposed canopy branches at river edges, sometimes in full sun. Nest-sites (see Breeding) are like day roosts, usually on branches that are at least as thick as the bird.

General Habits

Potoos are nocturnal and, under normal conditions, will not fly during the day. They spend their days perched still in the trees, upright on horizontal branches or at the tips of broken stubs, sometimes in exposed and conspicuous places. While resting, a bird has its eyes closed, its head hunkered on its shoulders, and its bill held horizontal so that it is almost unnoticeable, the loose body feathers masking anything birdlike in the potoo's form. With its cryptic plumage, the effect is of a dead stump, a lump of fungus, or a termite mound in a tree. If disturbed, perhaps detecting movement through the small slits in its eyelids, it assumes a "freezing" posture with the body elongated, feathers pressed down flat, neck upstretched, and bill held nearly vertically overhead, with the suggestion of a small "horn" erected over each eye. In this pose, it resembles a broken branch even more strongly. This is the posture most often illustrated, because it is the way most potoos are seen. The transition from resting to freezing is so smooth and gradual that, although it may occur in front of an observer, he will usually not detect any movement.

Roosting potoos barely move all day long; hence, they are known in Mexico by such local names as *bienparado* or "perfectly still", and *pájaro estaca* or "wooden stake bird". Occasionally one will stretch its wings, lean forward horizontally as if to stretch, or scratch its head with the foot brought over the wing. Individuals perched in the sun often sit with the bill open slightly, inconspicuously panting, with the head turned away from the sun. Because they do not need to open their big eyes to see movement, they rarely do so during the day. In fact, they rely so heavily on their camouflage that they can sometimes be approached and captured by hand before they will fly. A captured potoo will suddenly become animated, uttering a grotesque, croaking scream with its enormous mouth held open wide. Passing hawks may cause a potoo to "freeze", suggesting that hawks prey on potoos. For the most part, though, potoos are probably rarely bothered because their camouflage is so effective. Their cryptic plumage blends nearly perfectly with the colour and pattern of lichen-covered tree bark. Even the very differently coloured Rufous Potoo is beautifully camouflaged, its reddish tone blending with the colour of dead leaves, and its bright white spots like the flecks of sunlight that dapple the dark rainforest interior.

At night potoos do not seem particularly concerned with being cryptic. While scanning for prey from a perch, they look remarkably owl-like, the head turning rapidly from side to side, covering nearly 360°, or suddenly tipping up to follow the movements of some potential prey. With the head in its natural horizontal position, the eyes are directed slightly upwards, so objects above the horizontal are seen without effort. Potoos sing from the same exposed perches from which they forage, and are highly territorial, responding aggressively to playback of their songs.

The manner in which potoos can alter their appearance when perched is quite striking. The classic thin, inanimate-looking cryptic pose of this Great Potoo, with feathers sleeked flat and bill pointing high, in the past often erroneously interpreted as a sleeping posture, is in fact adopted only when the bird is disturbed; inevitably, this is the posture in which birds are most commonly seen. In contrast, a bird resting normally at the roost, or when active and hunting at night, has its feathers looser and relaxed, its head sunk into its shoulders, and its bill held level. The enormous eyes are not normally opened fully during the daytime, but this hunting Common Potoo clearly shows how the globular eyes bulge outwards and upwards, giving their owner an ample field of vision. Most species, like this one, have a bright yellow iris.

[Above:
Nyctibius grandis grandis,
Pantanal, Brazil.
Photo: Richard Matthews/
Planet Earth]

Below:
Nyctibius griseus griseus,
São Paulo, Brazil.
Photo: Ivan Szazima]

The main feeding technique used by potoos is that of a large, nocturnal and highly arboreal flycatcher. They make short sallying flights from an open perch, usually to take flying prey, though they will also fly to pick items off vegetation. Catching prey on the ground is evidently rare at best. This Great Potoo, perched on a snag in open woodland, can be seen in a typical alert foraging posture. Birds will also hunt in dense forest, where they are sometimes required to swoop acrobatically on their long wings.

[*Nyctibius grandis grandis*,
Llanos de Guárico,
Venezuela.
Photo: André Bartschi/
Planet Earth]



Next to nothing is known about potoo hygiene and maintenance. In a modest concession to cleanliness, a bird will lean forward and raise its tail slightly to defecate at an angle, avoiding staining the nest-site or day roost. The only preening observed has been an infrequent and rather lethargic bill primping of the breast feathers during the day, performed with the eyes characteristically closed. Reminiscent of the fur of sloths, the tail of some species can have a green stain on its tip or underside, apparently due to moss or algae growing on the feathers. Potoos are host to their own unique genera of parasitic feather mites (*Nyctibiolichus*) and lice (*Nyctibicola*).

As far as known, potoos always roost solitarily. At night, it is not uncommon to hear two singing birds in the same general area, quite possibly members of a pair. However, pair members are rarely seen together and then only briefly, even near the nest. In Trinidad, where the Common Potoo has unusually dense populations in the mangroves, and many individuals can be seen in a short period at nightfall, up to three birds have been seen foraging within sight of each other.

Because they are nocturnal, cryptic in plumage and behaviour, and live in the canopy of dense and remote forests, potoos are among the least studied of birds. What little is known about them is based mostly on museum specimens, themselves rare in collections, and on few observations of few species. Much of the information included here is from recent, unpublished observations by the present author and colleagues. Current fieldwork in the Neotropics is gradually improving our understanding, especially now that potoo voices are better known, making the birds easier to detect and locate.

Voice

Much more often heard than seen, potoos are best known by their haunting songs. Some species have more or less pure-toned songs sounding like whistles; others have a rougher, raspy, or even croaking quality. In Trinidad, the Common Potoo is called the "Poor-me-one", a more or less onomatopoeic interpretation of its song, meaning "Poor me, all alone". This is the most plaintively beautiful of all potoo songs. The experience of hearing a Common Potoo in a rainforest bathed in moonlight is one that marks its listener for life. The combination of eerie melancholy and mys-

tery surrounding potoos make hearing their song one of the quintessential Neotropical experiences.

Potoos sing most on moonlit nights, especially within a few days of the full moon, and at twilight. Apparently, the dim light conditions at these times are what most stimulate song. As with most birds, their song is a form of territorial advertisement. Playing back a tape recording or imitating a singing bird will usually bring that bird in close, even from a considerable distance, and is one of the few dependable ways of seeing a potoo. In response to playback, birds may sing continuously from a perch almost directly overhead and sometimes utter short calls while apparently searching for their imagined rival. Call notes are also given by both members of a pair to establish contact. Both males and females sing, although females may utter a weaker version of typical song, and males normally respond more aggressively to playback.

Vocalizations play an important part in potoo taxonomy (see Systematics), sometimes even serving as the sole basis for distinguishing species, as is the case with Northern and Common Potoos. Populations that were for a long time considered a single species occurring throughout the Neotropics are now recognized as containing two distinct vocal types, one in northern Middle America, and the other adjacent to it in southern Middle America and throughout tropical South America. In Costa Rica, where both vocal types occur and seem to segregate geographically, no distinct morphological differences have been found that correspond with the abrupt vocal shift. The differences in song are assumed to represent genetically distinct populations, not local dialects that are due to song learning from parents or neighbours. Also, it is assumed that representatives of the different song groups, if they came into contact, would treat each other as distinct species, not reacting to songs of the other type and not interbreeding. Although these are all probably reasonable assumptions, none has yet been tested.

The extent to which vocal differences represent populational genetic differences is not always clear. Striking differences in song helped to confirm the distinct species status of Andean and White-winged Potoos. On the other hand, without strong pressure from natural selection, voice could be subject to the same conservatism as found in potoo morphology. Thus, a lack of vocal distinction between geographically isolated populations may not signify a lack of genetic divergence. In the case of the Long-tailed Potoo, the Amazonian and Atlantic forest subspecies differ more morphologically than do other



The nest of this Common Potoo is in a typical site, being no more than the knot-hole of a broken-off branch. As rather large birds breeding in exposed sites, and with a nesting period lasting about three months in all, camouflage and cryptic behaviour are even more important to potoos when they are breeding than at other times. Thus all activity at the nest is minimized: the sitting adult perches on the edge of its nest, with its belly feathers fluffed forward over the egg or chick; nest change-overs take place only twice a day; and the chick is fed just a few times during the night.

[*Nyctibius griseus*, Cuyabeno Faunal Production Reserve, eastern Ecuador. Photo: François Savigny/ BBC Natural History Unit]

potoo subspecies, but are reported not to differ vocally. Also, it is crucial to distinguish the variations in voice produced by a single individual, or among individuals or between sexes within a species, from actual population genetic differences. The subtle vocal differences suggested by L. I. Davis to indicate the full species status of both *N. jamaicensis abbotti* and *N. griseus cornutus* need further study, to establish that they are not merely the product of single or few unusual individuals or of particular behavioural contexts.

Considerable progress has been made recently in identifying the mysterious sounds of night birds. The songs of all currently recognized potoo species are known. Nevertheless, there are numerous Neotropical night sounds reported, the source of which has never been identified; some of these may be potoo vocalizations. Also, potoo vocal repertoires are probably more varied than is presently known. Distinctive vocalizations associated with courtship, disturbance, and chick begging calls have been recorded in only a few species, but probably all species have them. Within any species, very little has been documented in the way of geographical variation in songs, and complicated cases, like that of the Northern and Common Potoos, require much more detailed study. With the White-winged Potoo, only the voice of the Amazonian form is known; birds of the population in Brazil's Atlantic forest have never been heard knowingly, nor has any individual been seen alive. As has been found in other potoo species, morphological resemblance is no guarantee of vocal similarity.

Food and Feeding

Potoos eat flying insects. They forage during the crepuscular period and at night, mostly by sallying from exposed perches much in the manner of many Tyrannidae: they fly up into the air to intercept and catch their prey one by one, returning to the same or another perch between attacks. This is also similar to the foraging of nightjars, except that potoos initiate their sallies from arboreal perches, never from the ground. A typical sally may range from less than one to several metres and is usually directed upward or horizontally on a more or less straight path. In aerial pursuit of prey, potoos can be surprisingly acrobatic on their long wings, even in dense forest. A Long-tailed Potoo, one of the largest species, was observed chasing flying termites in the rainforest understorey by making short sallies, turning abruptly to return to

its perch or suddenly twisting and changing directions in pursuit; yet it never even brushed its great wings or tail against the crowded vegetation or made a single sound.

Potoos will sometimes fly to vegetation to pluck off a perched insect. Unlike frogmouths and owlet-nightjars, potoos apparently do not drop to the ground after prey. A large katydid, being chased by a Great Potoo, closed its wings and fell straight to the ground, at which point the predator stopped its chase and, turning around abruptly in mid-air, returned to its high perch; from there, it completely ignored the katydid, although the insect remained on the ground in an open and conspicuous spot. The presence of beetle larvae and pieces of wood in the diet of one Northern Potoo suggests that potoos may occasionally investigate rotten trunks, although how they exploit this substrate, from the air or perched, is not known.

The commonest prey are beetles, including fireflies. Potoos also eat other night-flying insects, especially ones that fly slowly on fairly straight or predictable paths, including moths, true bugs, large orthopterans, and neuropterans. Flying termites constitute a favourite food during one of their hatches, when they are consumed in large quantities by potoos, as they are by most rainforest insectivores. Although their disproportionately large mouths enable potoos to take large prey, the bulk of their diet is composed of remarkably small items, and it is often impossible for an observer to detect the target of a given foraging attempt.

Potoos engulf their prey whole on the wing and are not known to beat it or to manipulate it in any way with their feet. The "teeth" on a potoo's bill may help to secure or break the wings of large prey, if they extend beyond the potoo's gaping mouth when captured. It is difficult to imagine how potoos swallow hard-bodied prey like beetles, which often have horns, spines, powerful mandibles and claws, without hurting themselves. Their jaws are too weak and the bill too delicate to crush such prey. However, the soft mouth and throat are lined with a tough and flexible skin that probably helps immobilize prey. Remarkably, a White-collared Seedeater (*Sporophila torqueola*) was found in the stomach of a Northern Potoo! Presumably, the little bird was taken after being flushed off its perch at night.

Although they rarely have any fat in the furcula or elsewhere on the body, potoos typically have large amounts of fat in the abdominal cavity. The reason for this is unknown. Perhaps the fat is a natural by-product of digesting their particular prey. It could

also be an adaptation for surviving short periods without food, such as rainy nights when few insects are flying or during the new moon when nocturnal visibility may be limited to dawn and dusk periods. Supplementing diet from fat stores might allow reduced foraging frequency, which could be advantageous to a bird whose primary form of defence is to remain still and camouflaged, especially during the prolonged nesting season (see Breeding).

Breeding

Considering how little is known about potoos in general, a surprising amount has been published on their nesting. Because a potoo nest, once found, is easy to observe, some accounts involve prolonged and detailed description. The total number of nests studied still amounts to only a handful, mostly of Common and Great Potoos, but the similarities among them (including observations of a Rufous Potoo nest, as yet unpublished) suggest that the following description may be generalized to all potoos.

Potoos are monogamous, both parents participating actively throughout the nesting period. Although the duration of the pair-bond is not known, nonetheless given the long duration of nesting and the fact that individual potoos maintain long-term territories, it is likely that pairs stay together on a long-term basis. On one occasion, a female apparently solicited mating by uttering an unusual vocalization, immediately attracting the male to her perch where they briefly copulated. Nothing is known about selection of the nest-site: how or when the site is chosen, by which member of the pair, or whether nest-site plays a role in mate selection or in territory location and size.

Potoos do not build a nest, but rather choose a natural depression in a tree, to which they apparently add no nesting material whatsoever. Typically, the nest is in the scar left on a branch or trunk where an upward-pointing branch died and fell off, or on top of a broken stub. One nest was in the tip of a slender dead palm stem, where the natural segmentation of the stem (as in bamboo) left a hollow just large enough for the single egg. The depression must be shallow enough so that part of the egg sits above it and can be incubated, but deep enough so the egg will not roll out. Although the female surely lays her egg directly in the nest, the spot appears so precarious that it has even been suggested that the egg is laid elsewhere and later carried to the nest in the adult's capacious mouth! The egg appears not to be stuck to the nest in any way, as is sometimes supposed, but also is not known to be turned or manipulated at all by the adults. Its shape is elliptical, averaging roughly 1.4 times longer than wide, and with one end broader than the other. Overall coloration is white with dark purplish-brown spots, most densely distributed near the broad end. Egg size for the smallest species is not known, but those eggs described to date range from roughly 36 x 26 mm for the smallest Common Potoo egg to about 52 x 38 mm in the Great Potoo. Clutch size, as far as known, is always one egg.

Both parents participate in nesting. It is impossible to identify the sex of the parents by their outward appearance and usually is hard even to distinguish one parent from the other. Nevertheless, specimens collected on nests during the day have turned out to be males. The parent that incubates in the day, presumably the male, stays all day without leaving the nest. At nightfall and before dawn, the parents switch roles. Sometimes the switch is made seamlessly, and on other occasions there can be a brief period when no adult attends the nest, during which time both parents are probably foraging. This timing may depend in part on whether the arriving bird has eaten enough yet when the other decides to leave, and on whether weather conditions permit the bird on duty to leave before the other settles in. In any case, the parents often give soft calls during this period, so vocal as well as visual cues may alert the sitting parent to the presence of the other.

The incubating or brooding parent perches at the edge of the nest in a normal resting position giving no sign that it is on a nest. The egg, and later the chick, disappears under the belly feathers of the adult. Normally the chick and brooding adult face in the same direction, and only after the chick is fairly large does it begin to become visible, poking out among the adult's breast feathers. Once the nestling has grown feathers covering its body,

the adults leave it for longer periods and take turns brooding through the night. Eventually, when the chick is too big for an adult to perch with it comfortably, the adults stop brooding. At this point, they may perch near the chick in the same tree or elsewhere out of sight, presumably nearby.

The chick is fed only a few times during the night, mostly just after dusk and before dawn. The parents feed by regurgitation, landing at the nest, looking upward while choking up food, and then tipping the head down to the nestling with open mouth, into which the chick lunges. Each arrival of an adult at the nest usually results in one or at most three feedings. Feeding frequency decreases as the chick grows, although possibly the quantity of food delivered increases.

Camouflage and inconspicuousness are the rule in potoo nesting. Infrequent feedings, limited activity, and infrequent vocalizing at the nest are probably adaptations to limit drawing attention. One Common Potoo was reported singing repeatedly from the nest, but in other cases singing was only heard away from the nest. Anything larger than a small bird near the nest may cause the adult to assume its alarm posture. Only as a last resort in defence of its young will a nesting adult potoo give up its dead stump imitation to frighten off a potential predator. If approached too close, first it will open its huge, bulging eyes and then suddenly lunge, snapping open-mouthed. Although unlikely to inflict any damage with its strike, this is a startling and intimidating display, especially coming from an object that moments before looked like a stick! Adults flushed from the nest during the day have given distraction displays, feigning a broken wing and sometimes even falling to the ground. A pair near their nest at night vocalized conspicuously and took turns flying short distances until they had led the observer several hundred metres through the woods away from the nest, at which point they became silent and flew off.

As the chick grows, it increasingly gives begging calls; these are single, buzzy notes and are hard to locate. At a fairly young age, the developing chick begins to assume the freezing posture when disturbed. If approached closely by an intruder, however, it will also lunge at it with open bill in mock strikes. Otherwise, the chick is extremely still, looking more like a lump of fungus

The Great Potoo chick sits tight in its knot-hole nest for some two months before it finally fledges. While peacefully perched, both adults and young will perform light rocking movements, perhaps in order to take a little exercise in a most inconspicuous way. The chick soon starts to adopt the adult's stiff upright posture if there is a source of danger or disturbance present, but, surprisingly, the near-white juvenile plumage of this species does not seem well suited to the crypsis on which it appears to depend.

[*Nyctibius grandis grandis*, gallery forest of the llanos, central Venezuela. Photo: Russell Thorstrom]





than a bird. Both nesting adults and nestlings have been observed to make a gentle rocking motion periodically at the nest. This may be a way to increase circulation without drawing attention. Eventually, shortly before fledging, the chick begins sessions of wing beating, mostly at night. Newly fledged young will perch near the nest for some days after their first flight, but seem to make no effort to return to their long-held position at the nest.

The incubation period can last at least one month and the fledging period over two more months after hatching. This is one of the longest nesting periods of any landbird. Even after leaving the nest, the fledgling is not adult size and continues to beg and be fed by the adults. This slow development, with limited activity at the nest shared by both parents invested in a single chick over a prolonged period, is consistent with the economy of movement characteristic of potoos, and attests to the success of their cryptic behaviour. A few cases of egg loss or chick disappearance and subsequent nest abandonment have been reported, but the presumed nest predator was not observed.

Nesting seasonality in potoos is poorly understood. Reports of nesting at the same location two and three years in a row at the same time of year suggest that nesting is seasonal and annual. Across the geographical ranges of Great and Common Potoos, however, these species appear not to be consistent in the time of year or season (wet as opposed to dry) during which they nest. A possibility worth examining is that factors such as the amount of annual rainfall and seasonal abundance of insect prey are related to nesting seasonality. In areas of very heavy rainfall, prolonged and forceful rains in the wet season may endanger chick survival and decrease available foraging time for adults, making dry season nesting preferable. On the other hand, insect abundances are usually greater at the start of the rains, when nesting might be expected to occur in drier regions, where the rainy season is milder. Multiple brooding is not known in potoos, and the length of the nesting period makes their producing more than one brood per year seem unlikely, especially if nesting is indeed seasonal.

The nest itself is apparently not used as a roosting site outside the nesting season, either by the adults or by the chick once it has fledged. Repeated nesting at the same site, however, sug-

gests that a good nest-site, although requiring no particular construction effort by the parents, may be hard to find. Considering that nest-sites are typically where some part of a tree has been damaged, either at a broken vertical stub or at the knot-hole where a branch has fallen off completely, such sites are probably often subject to rotting and may be short-lived. After one year, the dead and broken-topped palm stem where a Rufous Potoo had nested was so decomposed and fragile that it could not sustain even a gentle touch without breaking, much less the comings and goings for months of a pair of nesting birds. Despite not adding any material to a nest-site to improve its quality, adults seem to choose remarkably consistent kinds of locations for nesting. Given the rather exact specifications a nest-site must meet and the site's probably brief useful lifespan, the availability of nest-sites could be a limiting factor in potoo population density.

Movements

As far as is known, all potoo species are sedentary. In most cases, they probably maintain permanent territories all year round. Potoos can be found consistently at known sites for years, often at the same favourite perches. On the other hand, the Common Potoo in Costa Rica is known to occur only sporadically at certain sites. This may reflect local variability in resource quality or unstable population density near the limit of the species' range, rather than any large-scale movements.

Home range size is unknown. It may simply be noted that playback of vocalizations can attract a singing individual over several hundred metres. Post-fledging dispersal of young potoos from natal territories is, as with most birds, entirely undescribed.

Presumed vagrancy has been reported three times in potoos. There are two records of Northern Potoos from the tiny Caribbean islands of Mona and Desecheo, west of Puerto Rico; the nearest resident population is in Hispaniola, roughly 100 km away over open sea. Whether those vagrant birds arrived under their own power or were assisted by ships, as suggested by the following case, is a matter for speculation. A bird identified as a Common Potoo was seen flying around a ship sailing through the Panama Canal at dusk. As the ship pulled into harbour in Florida several days later, the bird was seen again, circling the ship before flying off in the direction of the mainland.

Relationship with Man

Potoos have fascinated man mostly for their mysteriousness. Even in their normally dry, technical writing, ornithologists often wax poetical and romantic on the subject of potoos. A. F. Skutch wrote that potoo calls "stir the imagination" and quoted lines from the poet Shelley. S. L. Hilty and W. L. Brown, in a field guide, described potoos as "so poorly known they seem more fiction than substance, their gruff or wailing cries ghostly delusions of the dim nocturnal world they inhabit". Although the genus name *Nyctibius*, meaning active or hunting at night, is not especially inspired, the choice of *aethereus* ("ethereal") for the Long-tailed Potoo is more representative of people's reactions to potoos. In parts of rural Colombia, potoos are called *mira para el cielo*, meaning "looks at the sky".

Local peoples in the range of potoos sometimes misidentify the familiar night voices of potoos as other animals. The voice of the Common Potoo is attributed to a sloth in some places, elsewhere to the pygmy anteater (*Cyclopes didactylus*). In the Brazilian Amazon, the song of the White-winged Potoo is often thought to be given by the *curupira*, a mythical forest spirit that protects animals from hunters.

Potoos, even when recognized as such, are surrounded by legend. The Common Potoo, in Brazil called *mãe-da-lua* ("mother of the moon") or *urutau*, is often believed to be the reincarnation of one of a pair of separated, widowed, or unrequited lovers whose sad lament is the bird's melancholy song. The songs of other species often inspire fear, and that of the Great Potoo is sometimes considered a sign of bad luck or impending death. For reasons unknown, potoo feathers have sometimes been attributed the power

The large size and long wings and tail of the Long-tailed Potoo make it an unlikely, if effective, flycatching species of dense forest interiors, as well as of more open woodland. Though not in danger on a global scale, as a species of primary forest it is locally threatened wherever such habitat comes under pressure, as for example in the Atlantic coastal forest of central South America. An adaptation of potoos which appears to be related to roosting is the presence of two or three notches which form peep-holes in the bird's upper eyelid: these may allow the bird to see approaching danger without having to risk opening its large and conspicuous eyes.

[*Nyctibius aethereus longicaudatus*, Amazonian region of Ecuador.
Photo: Russell Thorstrom]

to insure chastity. In rural Brazil, a potoo used to be killed and skinned for use in a ceremony intended to ward off seduction. Daughters at the beginning of puberty were made to sit on the potoo skin for three days while receiving worldly advice from their elders. More recently, and perhaps still to this day, potoo feathers were simply swept over the legs and hammock of the maiden to be protected or the bride whose fidelity was to be guaranteed. This power of potoo feathers, or perhaps merely their decorative value, may explain their occasional use in the ornamental garments of Amazonian Indians, including a necklace from Brazil made entirely of potoo feathers of several species.

Throughout the range of potoos, people living by subsistence will eat virtually any animal, and there are occasional reports of people eating potoos. However, potoos offer relatively little meat for their size and do not appear to be especially prized.

Status and Conservation

Potoos are extremely inconspicuous, appear to have few natural predators, and are not directly persecuted by man. On the other hand, they are not abundant anywhere, usually occur at low densities, and, for the most part at least, appear to be sedentary. These characteristics make them naturally vulnerable to the onslaught of human-caused habitat destruction. They are only as threatened as the forest habitats they occupy. Unfortunately, forests throughout the Neotropics are under constant assault from logging and agriculture, from governmental development projects, and from the ever-increasing numbers of landless poor. The first step of modern human expansion into areas of natural habitats continues to be deforestation or burning, resulting in what is often permanent unsuitability of those areas for continued occupation by native species.

No potoo species is currently listed as threatened, but several deserve special attention. The White-winged Potoo, although widespread in Amazonia, continues to be entirely unknown in life in the Atlantic forest, since it was first found there about 180 years ago. The Atlantic forest population, which is distinct from the Amazonian and may even be a separate species, if not extinct is probably limited to tiny patches of remnant forest. Before its near-total deforestation, the Atlantic forest was a heterogeneous

area composed of many different forest types, so it cannot be assumed that this species occurred throughout the entire region. Nevertheless, all areas should be searched intensively. The region from which it was originally described, presumably between the cities of Vitória da Conquista and Salvador in the Brazilian state of Bahia, is now dominated by cacao plantations. These plantations have historically left the largest forest trees intact, while replacing the understorey with plantations of cacao. It is possible that this potoo persists in the canopy of these areas, as do a number of other species with Amazonian affinities. Unfortunately, a recent blight affecting cacao plantations has caused many growers to switch to other activities, cutting down the remaining tall trees on their lands. Thus, the Atlantic forest's form of the White-winged Potoo should really be considered highly endangered, possibly extinct.

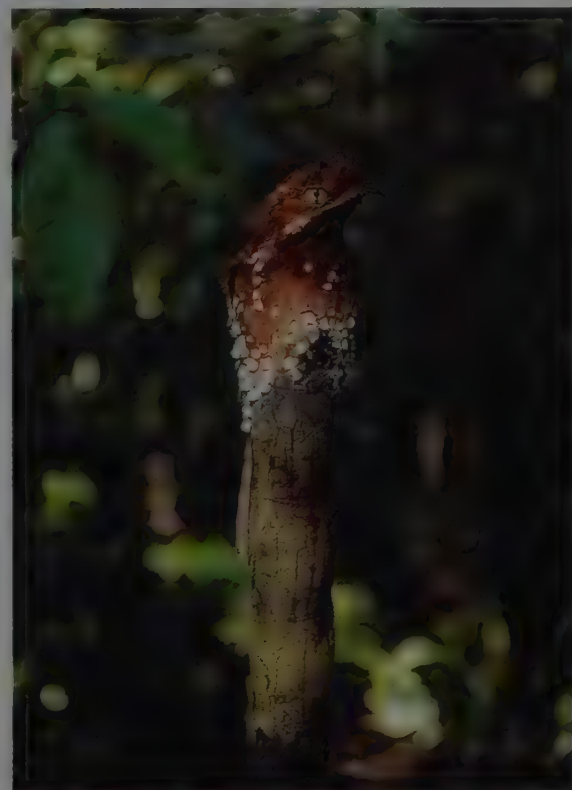
Similarly, the Atlantic forest population of Long-tailed Potoo is quite distinct from equatorial forms and may deserve recognition as a separate species. Although known from widespread localities, it appears to be rare and is probably quite limited in its current distribution. As with the entire Atlantic forest fauna, these birds must be vigorously protected. The Chocó form of Long-tailed Potoo, which is virtually unknown in life, and the Andean Potoo, which occurs in a fairly narrow elevational range on the humid slopes of the Andes, both have limited distributions and as such, although not in immediate danger, should be considered vulnerable. The Northern Potoo seems to be the most tolerant of man-altered habitats; nevertheless, this could simply be a result of the extreme lack of pristine environments in Middle America. Studies are needed to determine whether individuals found in disturbed areas represent breeding populations or mere stragglers from diminishing areas of preferred habitat.

Amazonian potoo species are in no immediate danger, because there are still huge expanses of primary forest in the Amazon. Nevertheless, habitat destruction in the Amazon continues apace, and it is only a matter of time before the situation becomes critical. Even in the most remote areas, due to international demand for timber, logging threatens pristine forests. Furthermore, recent recognition of the high levels of intraspecific genetic differentiation in potoos raises the possibility that traditional species limits do not account for real levels of potoo diversity. For this reason, populations within every major biogeographical sub-region, such as the Guianan shield and the major Amazonian interfluvia, should all be treated as potentially unique and should be protected. Because much the same may prove true for most of the Neotropical bird fauna, large and vigorously protected parks must be established in every habitat in every bioregion throughout the Neotropics. Seen from this regional perspective, even some Amazonian taxa are under immediate threat. For example, south-eastern Amazonia is already heavily deforested and contains few protected areas, although its birds are particularly poorly known.

In general, potoos probably do not require conservation measures directed specifically at them. Rather, habitat protection focused on preserving unique vegetation types and known areas of endemism for other bird species should be sufficient for potoo conservation as well. However, given their naturally low population densities, preserving large areas of continuous habitat may be necessary to maintain viable potoo populations. Forest management should include leaving some snags, which are important roosting, foraging and nesting sites for potoos, as well as for many other species. Finally, we must remember that potoos are among the world's least-known bird families. Ecological requirements, microhabitat preferences, distributional limits, and perhaps even new taxa of potoos, along with most details of their natural history, remain to be discovered.

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The Rufous Potoo is, in appearance, the most atypical member of the family. In addition to its small size, it has strikingly coloured plumage, somewhat resembling that of the Oilbird (*Steatornis caripensis*), and a peculiar dark wedge in the lower part of its iris. This bird is brooding a young chick on the only nest of the species so far known, atop a thin broken palm stem. This poorly known species is restricted to primary forest in lowland Amazonia, where it appears to be uncommon and perhaps locally distributed.

[*Nyctibius bracteatus*, north of Manaus, Amazonas, Brazil. Photo: Mario Cohn-Haft]



1
variants



2

ssp aethereus



ssp longicaudatus



grey variant

ssp mexicanus

red variant



3



red variant

4

dark variant



typical variant



5



ssp jamaicensis



7



6

o abbotti

PLATE 25

inches 5
cm 13

Genus *NYCTIBIUS* Vieillot, 1816

1. Great Potoo

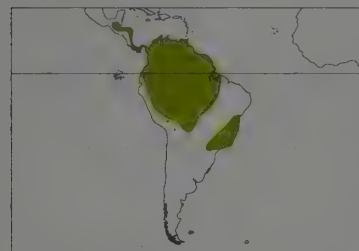
Nyctibius grandis

French: Grand Ibijau **German:** Riesentagschläfer **Spanish:** Nictibio Grande
Other common names: Grand Potoo

Taxonomy. *Caprimulgus grandis* J. F. Gmelin, 1789, Cayenne. Currently accepted races are doubtfully valid, and perhaps represent merely extremes in broad geographical size trends and individual plumage variation. No taxonomically recognized variation in most of extensive range, despite great genetic divergence on opposite sides of Andes and possible population disjunction between Amazonia and Atlantic forest; may contain undescribed "cryptic" taxa. Two subspecies tentatively accepted.

Subspecies and Distribution.

N. g. guatemalensis Land & Schultz, 1963 - extreme S Mexico, Guatemala, and possibly Honduras. *N. g. grandis* (J. F. Gmelin, 1789) - Nicaragua to N South America, where mostly E of Andes throughout Amazonia to N Paraguay, and in SE Brazil; may occur locally between Amazonia and Atlantic forest regions.



Descriptive notes. 45-55 cm; 500-620 g. Largest and bulkiest potoo, looking relatively big-headed and owl-like. Palest and most variable species in overall colour, ranging from buffy-brown to nearly white; iris brown. Sexes alike. Juvenile nearly pure white. Races weakly defined, mostly based on subtle, perhaps clinal, differences in size. **VOICE.** Song a harsh, sickly sounding "KWAAAHW", sometimes followed quickly by a similar, shorter note; given mostly on moonlit nights and during the crepuscular period. A few other short, guttural or barking calls have been described.

Habitat.

Canopy of lowland forested habitats, including tropical rainforest (both *terra firme* and *várzea*); gallery forest in areas of savanna or *cerrado*; and forest patches, old second growth, and tree plantations in moderately disturbed areas. Found most often along rivers and lakes. At night regularly ventures into clearings or open areas near forest to forage. Roosts during the day in canopy of large, often bare trees, where resembles a large pale stump or termite nest.

Food and Feeding. Feeds on beetles (Coleoptera), large katydids and grasshoppers (Orthoptera), and other flying insects; may sometimes capture small bats. Forages at night with flycatcher-like sallies from exposed perches in forest canopy or posts in clearings. Each sally may be several metres long, directed at a single flying prey item; bird often returns to same perch after sally.

Breeding. Presumed monogamous. Nesting noted at various times of year with no described pattern of seasonality. Nest usually located at bend or along upper surface of heavy, horizontal or diagonal branch in canopy; no nesting material added; egg laid in knot-hole or natural depression just large enough to contain it. Lays 1 egg, white with dark brown, grey and lilac blotches, mostly near broad end. Male incubates during day; fledging period nearly two months.

Movements.

Presumed sedentary. **Status and Conservation.** Not globally threatened. Uncommon in closed-canopy forest; common or more easily detected in naturally semi-open habitat, such as in Venezuelan llanos. Supposed absence from the *cerrado* and *caatinga* regions of Brazil, between the great forested domains of Amazonia and the Atlantic coast, may be real or merely the result of undersampling in an area where densities may be naturally low, due to the scattered and local distribution of forest; possibly commoner and more widespread in this area before most of original forest cover was destroyed. Historical evidence suggests that the species once occupied Atlantic forest in NE Brazil, whence there have been no confirmed records in the last three centuries. Probably vulnerable in northern Central America and in SE Brazil, where little forest remains intact.

Bibliography. Cintra & Yamashita (1990), Clay *et al.* (1998), Davis (1978), Friedmann & Smith (1955), González-García (1993), Haverschmidt (1948, 1958c), Haverschmidt & Mees (1994), Hilty & Brown (1986), Howell & Webb (1995a), Land (1970), Land & Schultz (1963), Meyer de Schauensee & Phelps (1978), Monroe (1968), Ortiz & Carrión (1991), Penard & Penard (1910), Perry (1979), Perry & Slud (1980), Pinto (1938), Rangel-Salazar (1990), Rangel-Salazar & Vega-Rivera (1989), Rangel-Salazar *et al.* (1991), Remsen & Traylor (1989), Ridgely & Gwynne (1989), Ridgway (1914), Ruschi (1979), Rutgers & Norris (1972), Schubart *et al.* (1965), Sick (1951, 1953, 1993, 1997), da Silva (1995), Slud (1979), Snyder (1966), Stiles & Skutch (1989), Teixeira (1992), Terborgh *et al.* (1990), Tostain *et al.* (1992), Vanderwerf (1988), Wetmore (1968a), Young & Zook (1999).

2. Long-tailed Potoo

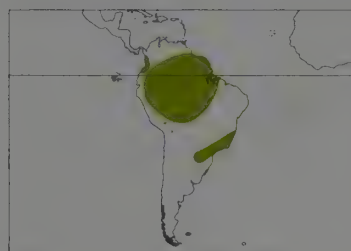
Nyctibius aethereus

French: Ibijau à longue queue **German:** Langschwanz-Tagschläfer **Spanish:** Nictibio Colilargo
Other common names: Large-tailed Potoo (*aethereus*, if two species recognized)

Taxonomy. *Caprimulgus aethereus* Wied, 1820, Rio Mucuri, Bahia, Brazil. Race *longicaudatus* (incorporating *chocoensis*) generally considered a distinct species for most of its recorded history, but recently lumped on rather scanty evidence; based on distinctive morphology, separate species status may be appropriate, although voices apparently similar. Relationships of all races require further study. Three subspecies currently recognized.

Subspecies and Distribution.

N. a. chocoensis Chapman, 1921 - Chocó region (W Colombia). *N. a. longicaudatus* (Spix, 1825) - scattered localities across Amazonia, probably throughout. *N. a. aethereus* (Wied, 1820) - Atlantic forest of SE Paraguay, NE Argentina and SE Brazil. A specimen from near mouth of R Amazon has been attributed to nominate *aethereus*, but probably erroneously.



Descriptive notes. 46-58 cm; 280-447 g. Long, strongly graduated tail, proportionately longer than in other species; species more rufescent overall than most congeners; conspicuous pale shoulder patch often present. Nominative race longer overall than bulkier *N. grandis*. Sexes alike. Race *chocoensis* darker, more richly coloured than similar *longicaudatus*; both considerably smaller and more rufescent than nominate, and proportionately longer-tailed. **VOICE.** Song a lethargic, plaintive, "ra-OOH" (with second syllable higher), repeated once every 5-10 seconds. Also, a series of short "woof" notes, like large owl. Voices of Atlantic and Amazonian races apparently very similar; voice of Chocó population unknown.

Habitat. Forests in lowlands, from very wet to relatively dry and gallery forest. Inhabits primary forest interior, from understorey to subcanopy, and edges; occasionally in open areas adjacent to forest.

Food and Feeding. Forages nocturnally like other potoos, consuming flying termites, moths and beetles. Appears clumsy and over-sized, making short, acrobatic sallies in the cluttered forest interior on its great wings and tail.

Breeding. Nesting reported Aug-Nov in Paraguay. Single spotted egg atop broken stub or fencepost. **Movements.** Presumed to be sedentary.

Status and Conservation. Not globally threatened. Very poorly known. Nominative subspecies probably threatened in Atlantic forest, where little original forest remains. Northern forms appear more likely to be overlooked rather than really rare; not threatened as long as extensive primary forest lasts; race *chocoensis*, however, has restricted distribution and is poorly known, so should perhaps be considered vulnerable.

Bibliography. dos Anjos *et al.* (1997), Bates *et al.* (1992), Bierregaard (1988), Brooks *et al.* (1993), Butler (1979), Canevari *et al.* (1991), Chapman (1921, 1926), Chebez (1994), Cohn-Haft *et al.* (1997), Collar & Andrew (1988), Greenway (1978), Hartert (1892), Hayes (1995), Hellmayr (1912), Hilty & Brown (1986), Laubmann (1940), Madroño & Esquivel (1997), Meyer de Schauensee (1966), Meyer de Schauensee & Phelps (1978), Ortiz & Carrión (1991), Parker, Donahue & Schulenberg (1994), Parker, Foster *et al.* (1993), Parker, Kratter & Wust (1994), Penard & Penard (1910), Pinto (1938), Salaman & Gandy (1994), Schubart *et al.* (1965), Sclater (1866a), Sick (1951, 1993, 1997), da Silva (1995), Snyder (1966), Stotz & Bierregaard (1989), Stotz, Fitzpatrick *et al.* (1996), Stotz, Lanyon *et al.* (1997), Straneck & Johnson (1990), Straube & Bornschein (1991, 1995), Wied (1820, 1830), Zimmer & Hilty (1997).

3. Northern Potoo

Nyctibius jamaicensis

French: Ibijau jamaïcain **German:** Mexikotagschläfer **Spanish:** Nictibio Jamaicano
Other common names: Common(!)/Jamaican/Antillean Potoo

Taxonomy. *Caprimulgus jamaicensis* J. F. Gmelin, 1789, Jamaica. Sometimes considered conspecific with *N. griseus*, with which it forms a superspecies; separation based on distinctly different voices. In Costa Rica, where both occur, there appear to be no consistent morphological characters to distinguish the two vocal types. The type specimen of race *costaricensis* comes from a region in Costa Rica where it is presumed only *jamaicensis* vocal type occurs, hence its placement within present species; most specimens previously attributed to *costaricensis*, however, including those from Caribbean slope of Nicaragua, probably represent the *N. griseus* vocal type. Mainland races *lambei* and *costaricensis* doubtfully valid, probably representing extremes in clinal variation, suggesting synonymy with *mexicanus*. Race *abbotti* once proposed to be separate species, based on longer song noted in sample of unspecified number of individuals. Thorough taxonomic revision needed. Five subspecies currently recognized.

Subspecies and Distribution.

N. j. lambei Davis, 1959 - Pacific slope of W Mexico. *N. j. mexicanus* Nelson, 1900 - E & S Mexico to El Salvador and Honduras, including Roatán I. *N. j. costaricensis* Ridgway, 1912 - Pacific slope of N & C Costa Rica, and possibly W Nicaragua. *N. j. jamaicensis* (J. F. Gmelin, 1789) - Jamaica. *N. j. abbotti* Richmond, 1917 - Hispaniola and Gonâve I.



Descriptive notes. 38-44 cm; 210-251 g. Within single populations, individuals vary from reddish brown to grey-brown; iris yellow. Sexes alike. Juvenile paler than adult. Mainland races weakly distinguished, based on subtle differences in size and overall darkness of plumage, possibly related to ecological factors such as humidity and latitude: dry-region forms paler, northerly forms larger. Races *jamaicensis* and *abbotti* similar to one another, with more conspicuous streaking on underparts than in mainland forms. **VOICE.** Song, in quality like that of *N. grandis*, but in pattern like that of *N. griseus*; a harsh, guttural, unmusical "bwaahawh."

"bwa-bwa-bwa"; up to ten final syllables in *abbotti*.

Habitat. Forest edge and open areas near forest or with scattered trees, including parks and farmland, even golf courses (Jamaica); humid and dry woodlands; lowlands occasionally up to 1500 m. Roosts during day in trees or atop poles. At night forages in open from fenceposts and snags.

Food and Feeding. Feeds on flying insects of all sizes, including Coleoptera, Homoptera, Hemiptera, Orthoptera, Lepidoptera and Neuroptera; one bird recorded eating a White-collared Seedeater (*Sporophila torqueola*). A nestling's stomach contained beetle larvae and bits of wood as well as more typical winged prey, all presumably fed to it by the parents. Forages nocturnally like all potoos, sallying from exposed perches after flying insects.

Breeding. Adults with enlarged gonads in Feb-Apr in Mexico and Belize; one May egg in Mexico; unfledged young in May in Mexico and Guatemala; nesting reported nearly throughout year in Jamaica, and Apr-Jul in Hispaniola. Nest is simple depression atop stub, where adult sits cryptically perched; site sometimes reoccupied in subsequent years. Lays 1 egg, white with grey, brown

and purplish blotches at wide end; male attends nest during the day, female at night, both parents feeding chick.

Movements. Presumed mainly sedentary; individual vagrants twice found on islands off Puerto Rico. **Status and Conservation.** Not globally threatened. Fairly common to rare and possibly local, but poorly known. In danger of extirpation in El Salvador; presumed presence in Nicaragua unconfirmed. Apparently tolerant of human-altered habitats, where some forest remains. Major threat is continued forest destruction throughout range. Health of populations in fragmented landscapes, such as those prevailing in most of range, not known; research and census work required.

Bibliography. Álvarez del Toro (1971), Anon. (1995a), Binford (1989), Bond (1985), Brodtkorb (1943), Cory (1886, 1918), Davis (1972, 1978), Dod (1987, 1992), Foster & Johnson (1974), Hardy & Webber (1975), Hartert (1892), Howell & Webb (1995a), Klaas (1968), Komar (1998), Land (1970), Lowery & Dalquest (1951), Monroe (1968), Paynter (1955), Raffaele (1981), Raffaele *et al.* (1998), Rand & Traylor (1954), Ridgway (1914), Rowley (1984), Russell (1964), Schaldach (1963), Sclater (1866a), Slud (1964), Smithe (1966), Stiles & Skutch (1989), Sutton (1950, 1951b), Thurber *et al.* (1987), Van Tyne (1935), Wetmore & Swales (1931).

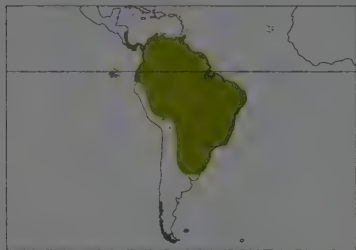
4. Common Potoo

Nyctibius griseus

French: Ibijau gris **German:** Urutau-Tagschläfer **Spanish:** Nictibio Urutáu
Other common names: Grey/Lesser Potoo

Taxonomy. *Caprimulgus griseus* J. F. Gmelin, 1789, Cayenne. Forms superspecies with *N. jamaicensis*, and these two sometimes treated as conspecific, although voices differ greatly. Costa Rican birds, originally all included in single race, *costaricensis*, now thought to include two species; because *costaricensis* is currently recognized as a race of *N. jamaicensis*, birds of present species in Costa Rica and elsewhere in N are referred to adjacent race *panamensis*, although they possibly represent an unnamed taxon. Invalid race *cornutus*, recognized by some earlier authors, is now considered synonymous with nominate race, despite proposal for full species status based on geographically limited sample showing subtle differences in voice. Two subspecies currently accepted.

Subspecies and Distribution. *N. g. panamensis* Ridgway, 1912 - Nicaragua and SW Costa Rica to N South America W of Andes, from NW Venezuela to W Ecuador. *N. g. griseus* (J. F. Gmelin, 1789) - Trinidad and Tobago; E of Andes from Colombia, Venezuela and the Guianas to N Argentina, N Uruguay and S Brazil.



Descriptive notes. 33-38 cm; 145-202 g. Nearly identical to *N. jamaicensis*, especially in area of contact, although averages smaller throughout range. Colour variation within populations ranges from reddish-brown to grey-brown. Sexes alike. Juvenile whitish. Races weakly defined, based on subtle, perhaps clinal, differences in size and overall coloration. Voice. Song a haunting, drawn out, descending series: "feeoo, foo, foo, foo, ..." of roughly 4-8 pure or slightly raspy notes; first "note" sometimes distinctly two-toned, dropping abruptly in pitch. Sings most at dusk, just before dawn, and on moonlit nights.

Habitat. Open woodland, especially near water; savannas and plantations with trees, *cerrado*, *várzea* and *terra firme* forest edges, second growth and mangroves. Roosts in trees in canopy and at edges; forages in open places from exposed snags and atop posts and stumps, often within few metres of ground, where vegetation is low. Mainly in lowlands, but occasionally up to c. 2000 m. **Food and Feeding.** Feeds on beetles (including large fireflies), moths, true bugs, mantids, flying ants and termites, cicadas, leafhoppers and grasshoppers. Forages mostly solitarily, at night, especially during the crepuscular period. Searches for prey from exposed perches, turning head rapidly from side to side, in owl-like way. Sallies like a flycatcher after night-flying prey, often returning to same perch.

Breeding. Throughout range as a whole nesting has been noted during every month of the year, with no general seasonal or annual pattern; however, in any given region, it tends to occur at roughly the same time each year. Nest is shallow knot-hole or depression at broken stub, situated at medium-height in tree; no nesting material. Lays 1 egg, with violet and brown speckles, densest at broad end; incubation 1 month or longer; chick is brooded for as much as 3 weeks; fledging 40-50+ days. Male incubates and broods during the day, rarely moving and relying on cryptic coloration and posture to avoid detection; female incubates at night after brief foraging period at nightfall; parents take turns brooding and feeding chick through the night.

Movements. Apparently sedentary, although perhaps not maintaining permanent territories. Reported to be of sporadic occurrence at certain sites in Costa Rica. Apparent absence outside breeding season in S of range may reflect merely seasonal singing, rather than migratory movements. One reported case of ship-assisted vagrancy between Panama and Florida, thought to refer to present species.

Status and Conservation. Not globally threatened. Fairly common to uncommon; biology and status not well known, despite being the most intensively studied potoo species. Less strictly tied to primary forest than most other species and so more tolerant of human disturbance; nevertheless, the chief threat is habitat destruction.

Bibliography. Anon. (1995a), Belcher & Smoother (1936), Belton (1984), Borrero (1970, 1980), Brooks *et al.* (1993), Canevari *et al.* (1991), Chapman (1926), Contreras *et al.* (1990), Davis (1978), French (1991), Fiebrig (1921), Fjeldså & Mayer (1996), Foster & Johnson (1974), Gochfeld (1973), Goeldi (1896, 1904), Hartert (1892), Haverschmidt (1958c), Haverschmidt & Mees (1994), Helme (1996), Herklots (1961), Hilty & Brown (1986), Johnson (1937), Kale (1982), Meyer de Schauensee & Phelps (1978), Muir & Butler (1925b), Narosky & Yzurieta (1993), Parker, Donahue & Schulenberg (1994), Parker, Kratter & Wust (1994), Parker, Schulenberg & Wust (1994), Penard & Penard (1910), de la Peña (1994), Phelps & Phelps (1956), Pinto (1938, 1953, 1978), Pinto & de Camargo (1948), Remsen & Traylor (1989), Ridgely & Gwynne (1989), Ridgway (1914), Robinson (1997), do Rosário (1996), Saibene (1987), Saibene *et al.* (1996), Schubart *et al.* (1965), Sclater (1866a), Sick (1951, 1993, 1997), Skutch (1970), Slud (1964), Snyder (1966), Stiles & Skutch (1989), Tate (1994), Tostain *et al.* (1992), Wetmore (1926, 1968a), Zimmer (1930).

5. Andean Potoo

Nyctibius maculosus

French: Ibijau des Andes **German:** Andentagschläfer **Spanish:** Nictibio Andino

Taxonomy. *Nyctibius maculosus* Ridgway, 1912, Ambato, Ecuador.

For some time was considered a race of *N. leucopterus*, which differs, however, in size, plumage, voice, and elevational distribution. Monotypic.

Distribution. Scattered localities in Andes from W Venezuela and E Colombia through E Ecuador and E Peru to NW Bolivia.



Descriptive notes. 34-38 cm; 145-195 g. Similar size to that of *N. griseus*; dark brown overall, never grey as in some individuals of *N. griseus*. Variable amount of white in wing patch, never as extensive as in smaller *N. leucopterus*. Iris yellow. Sexes alike. Voice. Song, given on moonlit nights from one of several preferred perches, repeated at roughly 10-second intervals: a raspy "ra-AH", higher on second syllable; like a fast, high-pitched song of *N. aethereus*. Short, descending, three-note call apparently given by female in courtship.

Habitat. Montane subtropical and temperate cloudforest with openings, at elevations of 1800-2800 m. Perches on snags in canopy.

Food and Feeding. Stomachs contained large insects, including beetles.

Breeding. One copulation observed in Sept in Ecuador. Otherwise unknown; presumed to be broadly similar to other potoos.

Movements. Presumed sedentary.

Status and Conservation. Not globally threatened. Very poorly known; may be fairly common locally. Extensive research and survey work needed in order to establish ecological requirements, as well as population densities and trends.

Bibliography. Chapman (1926), Fitzpatrick & Willard (1982), Fjeldså & Krabbe (1990), Greenway (1978), Hilty & Brown (1986), Kirwan & Sharpe (1999), Krabbe (1992), Meyer de Schauensee & Phelps (1978), Ortiz & Carrión (1991), Parker, Parker & Plenge (1982), Parker, Schulenberg *et al.* (1985), Remsen & Traylor (1983, 1989), Ridgway (1912a, 1914), Schulenberg & Aubrey (1997), Schulenberg *et al.* (1984).

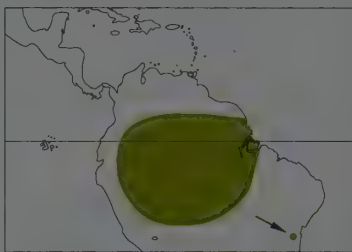
6. White-winged Potoo

Nyctibius leucopterus

French: Ibijau à ailes blanches **German:** Weißflügel-Tagschläfer **Spanish:** Nictibio Aliblanco

Taxonomy. *Caprimulgus leucopterus* Wied, 1821, near Conquista, Bahia, Brazil. Formerly considered to include *N. maculosus*, which differs, however, in size, plumage, voice, and elevational distribution. Includes two populations: Amazonian form is a new taxon, as yet undescribed, perhaps deserving species status. Currently treated as monotypic.

Distribution. Lowlands of Amazonia in N Brazil, S Guyana and distantly scattered unpublished localities, probably occurring throughout; also single site in E Brazil (type locality).



Descriptive notes. 24-29 cm; 77-85 g in Amazonia, weight of eastern form unknown. Relatively short-tailed; dark brown, paler below; conspicuous, large white patch across secondary coverts. Sexes apparently alike. Variability in extent of white wing patch and of reddish tones in brown may be age- or sex-related. Amazonian form much smaller than eastern, the two virtually identical in coloration. Voice. Haunting, melancholy, whistled song in Amazonia, given mostly on moonlit nights: a gradually descending, pure-toned "feeoooooooo" lasting c. 4 seconds; sometimes rising slightly at beginning. Call a soft, single or repeated "bweep".

Habitat. In Amazonia, canopy of primary lowland *terra firme* rainforest, including lighter forest on sandy soil. In E Brazil, habitat unknown; species presumed to occur similarly in canopy of primary Atlantic rainforest.

Food and Feeding. Small to medium-sized flying insects, including beetles, moths, cicadas, mantids, orthopterans, winged termites, and true bugs. Forages by sallying into air from exposed perches at night.

Breeding. Unknown. Habits presumed to be similar to those of congeners; nest probably situated in canopy.

Movements. Probably sedentary.

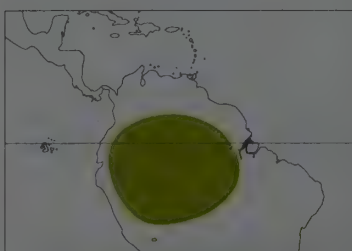
Status and Conservation. Not globally threatened. E Brazilian form is unknown in life, and probably limited to remnant patches of Atlantic rainforest, where it is highly threatened or possibly even extinct. Amazonian form, only recently discovered, has been found as being common to uncommon at scattered distant localities; probably occurs throughout Amazonia in appropriate habitat, where the biggest threat comes from continued destruction of pristine forest.

Bibliography. Chapman (1926), Cohn-Haft (1993, 1998), Cohn-Haft *et al.* (1997), Collar & Andrew (1988), Greenway (1978), Hartert (1892), Parker *et al.* (1993), Peres & Whittaker (1991), Schulenberg *et al.* (1984), Sick (1993, 1997), Wied (1821, 1830), Willis (1992).

7. Rufous Potoo

Nyctibius bracteatus

French: Ibijau roux **German:** Tropfentagschläfer **Spanish:** Nictibio Rufo



Taxonomy. *Nyctibius bracteatus* Gould, 1846, Bogotá, Colombia. Monotypic.

Distribution. Known from scattered localities in E Ecuador and E Peru to N Brazil and Guyana; probably occurs throughout lowland Amazonia.

Descriptive notes. 21-25 cm; 46-58 g. Smallest and atypically coloured potoo; overall deep orange-rufous coloration, with large white spots narrowly bordered in black, resembling Oilbird (*Steatornis caripensis*) and red morph of some *Aegotheles* species; long bristles ema-

nating from loral region; yellow iris has dark wedge in the lowest portion. Sexes alike. Juvenile plumage browner without white spots, more typical of adults of other potoo species. **VOICE.** Song a soft, rapidly descending series of roughly 10-15 notes: "bu-bu-bu-bu-bu-bu...", reminiscent of an *Otus* screech-owl or Amazonian Pygmy-Owl (*Glaucidium hardyi*). Call a single note, "wup", raspier than that of *N. leucopterus*. Another vocalization, "quaaw-co", for some time attributed to present species but almost certainly erroneously. **Habitat.** Occupies understorey and middle storey of primary lowland *terra firme* rainforest and also swampy palm forests. Can occasionally be found perching within 1 m of ground, but usually higher up. **Food and Feeding.** Consumes flying insects of orders Coleoptera, Orthoptera, Lepidoptera, Hymenoptera and Neuroptera. Forages like other potoos, with short upward- or outward-directed sallies, typically returning to same perch.

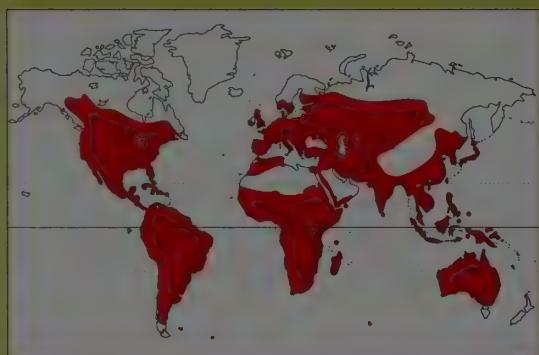
Breeding. Single nest known, from Brazil, occupied Sept to Dec: 1 blotched egg atop broken stub, inside rainforest; both adults participated in nesting tasks; fledgling, not yet adult size, still fed by parents away from nest. **Movements.** Presumed sedentary. **Status and Conservation.** Not globally threatened. Very poorly known; perhaps locally distributed, and probably not common. Probably not seriously threatened as long as extensive areas of Amazonian forest remain intact; needs further study to determine specific habitat preferences and distributional limits. **Bibliography.** Bierregaard (1988), Butler (1979), Cohn-Haft (1989, 1998), Cohn-Haft *et al.* (1997), Collar & Andrew (1988), Hartert (1892), Hilty & Brown (1986), Parker, Donahue & Schulenberg (1994), Parker, Parker & Plenge (1982), Penard & Penard (1910), Selater (1866a, 1866b), Sick (1993, 1997), Snyder (1966), Stotz & Bierregaard (1989), Stotz *et al.* (1996).

Class AVES

Order CAPRIMULGIFORMES

Suborder CAPRIMULGI

Family CAPRIMULGIDAE (NIGHTJARS)



- Small to large nocturnal birds, with variegated plumage, large mouth, long wings and tail, and short legs.
- 15-40 cm (with tail streamers, up to c. 100 cm).



- Cosmopolitan, although absent from polar regions.
- Desert, grassland and open wooded country to forest, from sea-level up to 4200 m.
- 15 genera, 89 species, 221 taxa.
- 6 species threatened; none definitely extinct since 1600.

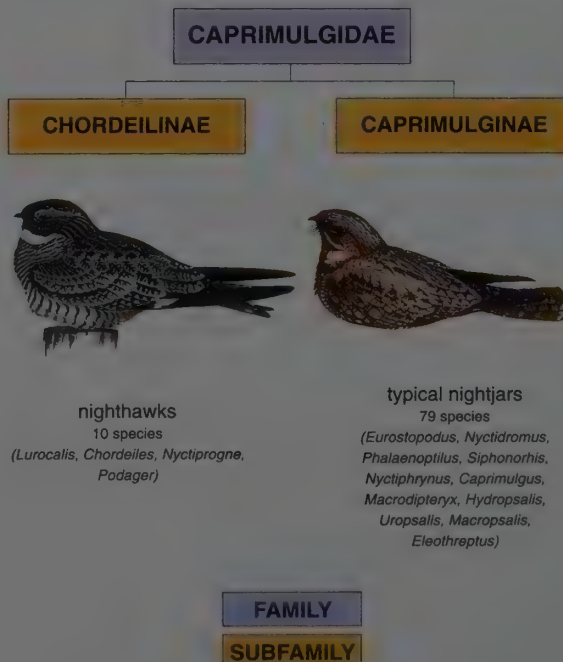
Systematics

The rather primitive-looking nightjars have probably arisen from ancient landbirds, but, despite the valuable fossil evidence now available, their true origins still remain unknown. Their earliest ancestors so far identified belong to an extinct family of ancient caprimulgid birds, the Archaeotrogonidae, that date back to the late Eocene some 40 million years ago. Originally considered to be fossil trogons that lacked the heterodactyl foot typical of modern trogons (Trogonidae), four species have so far been discovered in the Phosphorites du Quercy deposits in south-west France and have been placed in an extinct genus *Archaeotrogon*. One species, *Archaeotrogon venustus*, appears to have been more successful than the others, its fossil remains showing that it had a temporal span of approximately 14 million years. Two of the others do not appear earlier than about 32-30 million years ago during the Oligocene, and data for the fourth are insufficient for accurate dating. Fossil Caprimulgidae also date back to similar times, a species from the Upper Eocene of the Phosphorites du Quercy being placed in an extinct genus *Ventivorus*, and an as yet unidentified species taken from the Middle Eocene Messil oil shales clearly showing a characteristic nightjar-like foot. Fossil material from the much less distant Quaternary period is also well documented: apart from the Cuban species *Siphonorhis daiquiri*, apparently long extinct, and the Jamaican Poorwill (*Siphonorhis americana*), which might also be extinct, evidence is available for extant species from Europe, North and South America, Puerto Rico and Australia.

Since the 1750's, taxonomists have classified the various caprimulgiforms in many different ways, especially when attempting to determine their relationships with other birds. Frequently treated as relatives of the owls (Strigiformes) and the swifts (Apodidae), they have also been linked with hummingbirds (Trochilidae), trogons, todies (Todiidae), motmots (Momotidae), bee-eaters (Meropidae), rollers (Coraciidae), jacamars (Galbulidae) and puffbirds (Bucconidae), while another grouping often placed nightjars close to the swallows (Hirundinidae) within the passerines, with swallows formerly being considered relatives of the swifts. Superficial ties between nightjars and swifts are suggested by their adaptations to feeding, species in both families being aerial insectivores with wide gapes, while owls and nightjars share soft, variegated plumages and nocturnal habits, although several authorities put all of these similarities down to convergence. The scientific evidence, however, shows that

there are some morphological similarities which appear to confirm a phylogeny linking the owls, nightjars and other Caprimulgiformes (see below), and this is further supported by results from recent DNA-DNA hybridization studies.

During the second half of the eighteenth century, all caprimulgiform birds were assigned to the single genus *Caprimulgus*; it was not until the early nineteenth century that ornithologists realized that some of the species were so different that they actually belonged not only in separate genera, but also in separate families. Thus, by the 1830's, the Oilbird (*Steatornis caripensis*), the frogmouths (Podargidae), the owl-nightjars (Aegothelidae) and the potoos (Nyctibiidae) had been separated from the nightjars, although it was often recognized that, aside from their relationships to other birds, they were each other's closest relatives. From this time also, taxonomists began to separate the true nightjars into different genera, and it seems that the



Subdivision of the
Caprimulgidae

[Figure: Dave Nurney &
Angels Jutglar]

The nightjars comprise a fairly diverse assemblage of nocturnal aerial insectivores.

Of 51 different genera that have at various times been recognized within the family Caprimulgidae, only 15 are currently considered valid.

The Ocellated Poorwill belongs to the group loosely known as the poorwills. They are restricted to North and South America and are amongst the smallest of the nightjars, having shorter and more rounded wings than other species and extremely long rectal bristles.

[*Nyctiphrynus ocellatus*
ocellatus,

Manu National Park, Peru.
Photo: Michael Fogden/
Oxford Scientific Films]



only thing they could actually agree upon was that all members of the family were instantly recognizable as being nightjars. These changes in genera covered species in all parts of the world, although the greatest re-evaluation concerned the Americas, many authors arguing that all New World species differed from their Old World *Caprimulgus* counterparts. In all, 51 different nightjar genera have been named since 1758, although the number of genera considered valid currently stands at 15.

The so-called nighthawks are thought to have originated in South America and now breed throughout much of North America and the Neotropics. Nighthawks differ from nightjars in having a desmognathous palate, that of the nightjars being schizognathous; they differ further in generally lacking elongated rectal bristles around the gape, and in often being more active during the day. They are placed in a separate subfamily, the Chordeilinae, all other nightjars being placed in the subfamily Caprimulginae. Four genera of nighthawks are currently recognized: *Chordeiles*, containing six species, is the largest and most widespread; *Lurocalis* comprises two species; and both *Nyctiprogne* and *Podager* are monotypic.

The genus *Eurostopodus* comprises seven species that also lack prominent rectal bristles. Found in Australia, New Guinea, Sulawesi and many parts of Asia, these are fairly large birds that do not have white markings on the tail, while the majority of species also lack prominent white spots on the outer primaries. Two species also have elongated feathers on each side of the head, at the rear of the crown, from which the term "eared-nightjars" has been coined.

The New World poorwills are among the smallest of the nightjars, comprising seven species divided into three genera. They have brownish wings that are strongly banded tawny or buffish and lack white markings, and have most of their tail feathers tipped with white. *Nyctiphrynus* numbers four Central and South American species, including two endemic to Mexico and one endemic to the Chocó faunal region of Colombia. *Siphonorhis* contains two species, one endemic to Hispaniola, the other to Jamaica, although the latter may be extinct, not having been seen with certainty since the middle of the nineteenth century. The other genus within this group is the monotypic *Phalaenoptilus* of North America and northern Mexico. Loosely clumped alongside this group is the distinctive genus *Nyctidromus*.

The most widespread and species-rich genus is *Caprimulgus*, containing 56 species of "typical" nightjars that often have variegated plumages, white wing and/or tail markings (at least in males) and long rectal bristles around the gape. On the basis of main breeding ranges, Africa has the highest number, with 19 species, while Asia and South America have 12 each. Central America and the Caribbean islands are home to seven, Madagascar has two endemics, and North America and Europe have two apiece.

The Afrotropical genus *Macrodipteryx* contains two species, in which the males grow elaborate and elongated second (innermost) primaries prior to the breeding season. Finally, four distinctive genera are to be found in South America. These are *Hydropsalis* and *Uropsalis*, each containing two species, and *Macropsalis* with one species, all of which may possibly be closely related, and the monotypic *Eleothreptus*. The *Hydropsalis* nightjars are characterized by the unique tail shape of the breeding males, while *Uropsalis* and *Macropsalis* males have extremely elongated outermost tail feathers, the two groups possibly being linked by the male Scissor-tailed Nightjar (*Hydropsalis torquata*), which also has elongated outer tail feathers.

For many years, all *Lurocalis* nighthawks were thought to belong to one species, the Short-tailed or Semi-collared Nighthawk (*Lurocalis semitorquatus*), although the larger Andean form has different vocalizations and morphological characteristics and is now recognized as a distinct species, the Rufous-bellied Nighthawk (*Lurocalis rufiventris*). The Semi-collared's southern migratory form *nattereri*, sometimes known as the Chestnut-bellied Nighthawk, is also regarded as specifically separable by some ornithologists, although its similar vocalizations would suggest that further studies are needed if this split is to be convincingly justified.

The *Chordeiles* nighthawks are a distinct group of partially diurnal nightjars, occurring throughout much of North, Central and South America. Three species, the Common Nighthawk (*Chordeiles minor*), the Lesser Nighthawk (*Chordeiles acutipennis*) and the Least Nighthawk (*Chordeiles pusillus*), have vast breeding ranges and are subdivided into numerous subspecies. The Antillean Nighthawk (*Chordeiles gundlachii*) was long regarded as a Caribbean form of the Common Nighthawk, but its different vocalizations and its sympatric breeding on the Florida Keys confirm its status as

■ distinct species. The recently described Bahian Nighthawk (*Chordeiles vielliardi*), assigned to the genus *Chordeiles* on the basis of two museum specimens and brief vocal and behavioural evidence, has generated a certain amount of interest and comment, and recent field observations suggest that it might actually be more closely related to the Band-tailed Nighthawk (*Nyctiprogne leucopyga*). The Sand-coloured Nighthawk (*Chordeiles rupestris*) is the remaining member of this group and is highly adapted to life along the sandbars and riverbanks of large South American waterways. The Nacunda Nighthawk (*Podager nacunda*) is a distinctively large, boldly marked Neotropical species which remains within a genus of its own.

Those nightjars within the genus *Eurostopodus* are medium-sized to large birds that range from India east to China, and south through Sumatra, Borneo, Sulawesi and New Guinea to Australia, the Solomon Islands and New Caledonia. Evidence from recent DNA-DNA hybridization studies suggests that they may be sufficiently different from the rest of the Caprimulgidae to warrant placing them in a separate "sister" family, the Eurostopodidae, and the term "eared-nightjars" is increasingly being used when referring to species within this group. However, only two species, the Great Eared-nightjar (*Eurostopodus macrotis*) and the Malaysian Eared-nightjar (*Eurostopodus temminckii*), appear to have the "ear-tufts" at the back of the head, and they also differ from other *Eurostopodus* nightjars in their whistled call-notes, which are often given in flight, and in having ranges that extend into mainland Asia. Further studies may suggest that these two species be separated from the five "non-eared" nightjars; if so, the genus *Lyncornis* is available for them. The genus *Eurostopodus* was first used for the two species that occur in Australia, these being the Spotted Nightjar (*Eurostopodus argus*) and the White-throated Nightjar (*Eurostopodus mystacalis*). It is interesting to note that these two also show some morphological, vocal and ecological differences from their congeners, which begs the question whether the three remaining species, the Papuan Nightjar (*Eurostopodus papuensis*) and Archbold's Nightjar (*Eurostopodus archboldi*), both endemic to New Guinea, and Heinrich's Nightjar (*Eurostopodus diabolicus*), endemic to Sulawesi, are separable as a third genus. Two other island forms also require further study: birds on the Solomon Islands and New Caledonia are currently regarded as subspecies of the White-

throated Nightjar of Australia but may yet prove to be one, or even two, separate species.

Eight species classified in four genera occur only in the Americas. The Common Poorwill (*Phalaenoptilus nuttallii*) presents no real taxonomic problems. Nor does the Pauraque (*Nyctidromus albicollis*), although it was originally described as a *Caprimulgus* nightjar and was also tentatively linked with the *Siphonorhis* poorwills by some early ornithologists. Two species are placed in the latter genus: the possibly extinct Jamaican Poorwill and the Least Poorwill (*Siphonorhis brewsteri*) of Hispaniola. These are distinctive but poorly known species, with long tarsi, a wide bill and prominent, tubular nostrils. Although obviously closely related to the Jamaican Poorwill, the Least Poorwill was originally named in a separate genus, *Microsiphonorhis*. The four *Nyctiphrynus* poorwills are small, Neotropical nightjars about which very little seems to be known. Two species, the Eared Poorwill (*Nyctiphrynus mcleodii*) and the Yucatan Poorwill (*Nyctiphrynus yucatanicus*), are Central American endemics occurring mainly in Mexico, while a third species, the Ocellated Poorwill (*Nyctiphrynus ocellatus*), is found mainly in South America, although a small, rather disjunct population occurs in Central America. These three poorwills share several morphological features such as extremely long rictal bristles, dense crown feathers, and all but the central pair of tail feathers tipped white. The fourth species, the Choco Poorwill (*Nyctiphrynus rosenbergi*), is possibly worthy of further generic study as it differs from the other three in all of those respects.

The genus *Caprimulgus* encompasses most nightjar species and has representatives breeding in all of the world's faunal zones. Within the genus, there are many species that are obviously closely related to others, and at least ten groups of superspecies are possibly recognizable. Many other members of the genus show no immediate affinities with other nightjars, including probably a few that should not be classified as *Caprimulgus* nightjars at all.

Among the 21 New World species of *Caprimulgus*, there are possibly four or five groups of closely related nightjars covering 9-12 species. The first comprises the Chuck-will's-widow (*Caprimulgus carolinensis*) and the Rufous Nightjar (*Caprimulgus rufus*), which share similar plumages and vocalizations, while a second grouping covers two Caribbean endemics, the Cuban Nightjar (*Caprimulgus cubanensis*) and the Hispaniolan



Containing 56 species and spanning six continents, *Caprimulgus* is currently the largest and most widely distributed of the nightjar genera. It can be grouped into ten superspecies although ■ few taxa with no obvious affinities might best be allocated to separate genera. The Spot-tailed Nightjar perhaps belongs in this second category. It inhabits the grasslands, marshlands and scrub of South and Central America. While its long wings, tiny legs and variegated patterning are typical of the group, the unusual high-pitched call and tail-spotting of males suggest that it is not closely related to any other *Caprimulgus* species.

[*Caprimulgus maculicaudus*, Montsinéry, French Guiana. Photo: Jany Sauvanet/ NHPA]

For centuries, nightjars have been immersed in superstition and folklore as a result of their strange calls and mysterious nocturnal habits, and their shyness makes them extremely difficult to study. For instance, examination of current literature reveals almost nothing about the foraging behaviour or breeding biology of the Hispaniolan Nightjar. Several other species are known only from a few old specimens or rumours. Gradually, however, ornithologists are rediscovering missing taxa, using radio-telemetry to elucidate behaviour and recording the vocalizations of obscure species, thus facilitating their detection.

[*Caprimulgus ekmani*,
Zapotán,
Dominican Republic.
Photo: Alan Lewis]



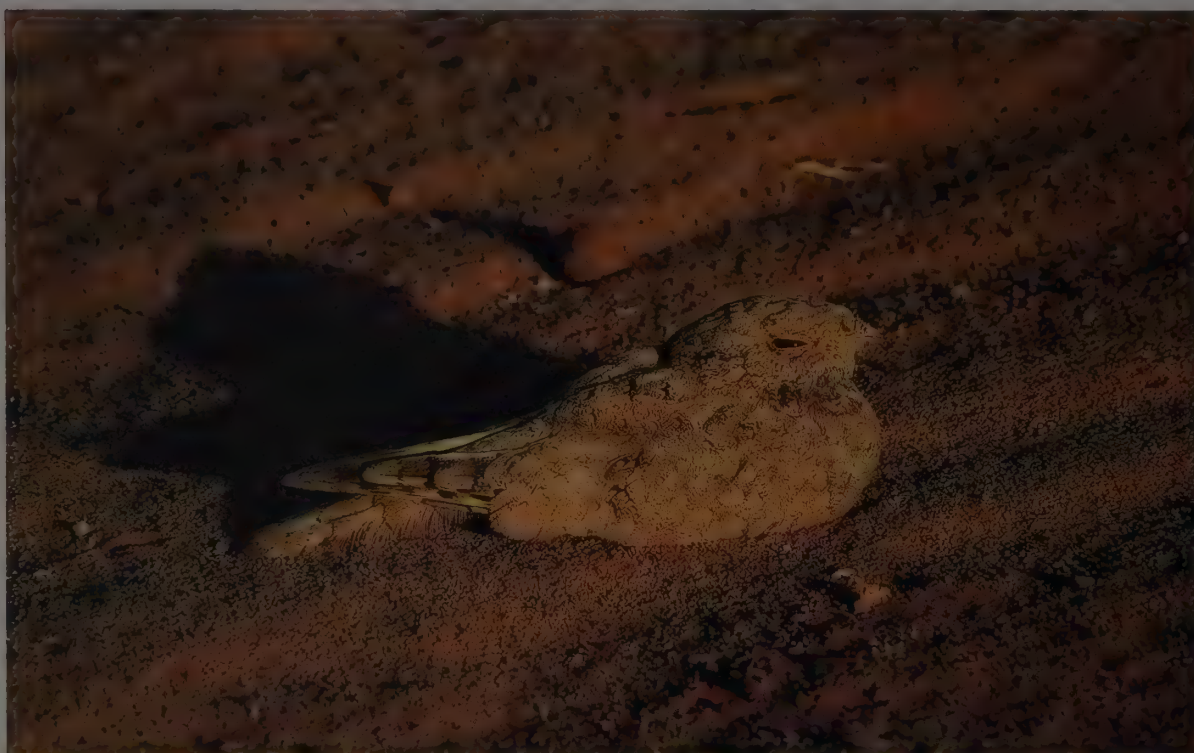
Nightjar (*Caprimulgus ekmani*), which until recently were generally considered to be conspecific. A third group links the Silky-tailed Nightjar (*Caprimulgus sericocaudatus*) of South America with two Central American endemics, the Tawny-collared Nightjar (*Caprimulgus salvini*) and the Yucatan Nightjar (*Caprimulgus badius*), all three again being considered conspecific at times. Two small, dark nightjars, the Blackish Nightjar (*Caprimulgus nigrescens*) and the little-known Roraiman Nightjar (*Caprimulgus whitelyi*), perhaps represent a further grouping; while yet another is possibly formed by the Whip-poor-will (*Caprimulgus vociferus*), the Puerto Rican Nightjar (*Caprimulgus noctitherus*) and the Dusky Nightjar (*Caprimulgus saturatus*).

Outside these close groupings, the Scrub Nightjar (*Caprimulgus anthonyi*) is endemic to the lowlands of western Colombia and Ecuador and until recently was considered to be conspecific with the widespread and fairly abundant Little Nightjar (*Caprimulgus parvulus*), the two not finally being recognized as separate species until the 1960's. The Cayenne Nightjar (*Caprimulgus maculosus*) is the rarest South American representative of the family, still known only from the type specimen, a male, taken in French Guiana in 1917. It is a small, brownish but nevertheless distinctive forest nightjar which, as some taxonomists have suggested, might be related to the Blackish and Roraiman Nightjar grouping.

Even less clearly related to other New World *Caprimulgus* species, the scarce and localized White-winged Nightjar (*Caprimulgus candicans*) perhaps does not belong in this genus. Described in the mid-1860's from two specimens, an adult male and a probable immature female, it remained something of a mystery until the 1990's, when birds began to be discovered at sites in Brazil, Bolivia and Paraguay. It has occasionally been linked with the White-tailed Nightjar (*Caprimulgus cayennensis*), possibly due to the amount of white in the tail of the adult male. However, examination of the type specimens, together with recent field observations, show that it exhibits several similarities to the Sickie-winged Nightjar (*Eleothreptus anomalus*), including the same sexual dimorphism, with males sharing some morphological features such as a generally cinnamon-based plumage and blackish, curved outer primaries, and females sharing a browner plumage and straighter, browner wings that are regularly barred tawny. Both species also appear to prefer grassland

habitats and have similar vocalizations and breeding habits, all of which supports the view that the White-winged Nightjar may actually be better placed in *Eleothreptus*. The remaining species found in the Americas are the Buff-collared (*Caprimulgus ridgwayi*), Band-winged (*Caprimulgus longirostris*), Spot-tailed (*Caprimulgus maculicaudus*) and Pygmy Nightjars (*Caprimulgus hirundinaceus*).

Among Afrotropical *Caprimulgus* nightjars, there are perhaps four groups of closely related species containing four, three, three and two members respectively. The remaining species in this region show no real ties with other nightjars, although the rare and almost unknown Prigogine's Nightjar (*Caprimulgus prigoginei*) looks remarkably similar to the Javan form *bartelsi* of Salvadori's Nightjar (*Caprimulgus pulchellus*), especially in the extent and shape of its wing and tail markings. One superspecies group contains species that generally inhabit wooded country and have whistled songs, although ornithologists are still divided as to how many species are involved. A common view is that there may be four in total: two lowland species, the Black-shouldered (*Caprimulgus nigriscapularis*) and Fiery-necked Nightjars (*Caprimulgus pectoralis*); and two upland ones, the Abyssinian (*Caprimulgus poliocephalus*) and Montane Nightjars (*Caprimulgus ruwenzorii*). A second group contains three species with churring songs: the southern African Rufous-cheeked Nightjar (*Caprimulgus rufigena*); the eastern African Sombre Nightjar (*Caprimulgus fraenatus*); and the European Nightjar (*Caprimulgus europaeus*), which has a breeding toehold in the extreme north-west of the continent. Another group of nightjars with churring songs comprises the Long-tailed (*Caprimulgus climacurus*), Slender-tailed (*Caprimulgus clarus*) and Mozambique Nightjars (*Caprimulgus fossii*). In the past, these three species were placed in their own genus *Scotornis*, being separable from *Caprimulgus* on the grounds of having graduated tail feathers, although the Mozambique Nightjar proved to be intermediate between *Scotornis* and *Caprimulgus* in having a slightly squarer, less strongly graduated tail. The final group comprises two species which superficially look very alike, the Plain Nightjar (*Caprimulgus inornatus*) and the poorly known Star-spotted Nightjar (*Caprimulgus stellatus*), although vocal and morphological differences, as well as their sympatric breeding range in East Africa, possibly invalidate their pairing as a superspecies.



Most nightjars have variegated plumage, the overall coloration of which tends to be related to the local soil or the habitat type frequented. The birds are most vulnerable during daylight when they roost on the ground, and cryptic plumage has evolved to minimize the likelihood of detection by diurnal predators. While many nightjars have conspicuous white patches in the primaries and outer-tail feathers, these are concealed when the tail is closed and the wing folded. Although deserts and semi-deserts with very little vegetation would appear to be a dangerous and unsuitable habitat for nightjars, several species have adapted to these harsh environments. This is reflected in the pallid and densely speckled plumage of the Egyptian Nightjar, closely matching the appearance of Saharan sand. Other species occur in dense vegetation and require much darker and more coarsely patterned plumage. The Pauraque, for example, displays a pattern of gold, black and rich brown that helps it to blend in with the leaf litter of Neotropical forests.

[Above:
Caprimulgus aegyptius
saharae,
250 km north-west of Lake
Chad, Niger.
Photo: Alain Dragesco/
Planet Earth.

Below:
Nyctidromus albigollis
albigollis,
Manu National Park, Peru.
Photo: Michael and
Patricia Fogden]



The remaining African species are: Bates's Nightjar (*Caprimulgus batesi*); the Freckled Nightjar (*Caprimulgus tristigma*); the Swamp Nightjar (*Caprimulgus natalensis*); Donaldson-Smith's Nightjar (*Caprimulgus donaldsoni*); the Golden Nightjar (*Caprimulgus eximius*); the Nubian Nightjar (*Caprimulgus nubicus*); the Egyptian Nightjar (*Caprimulgus aegyptius*), which also has a separate breeding population in Asia; the Red-necked Nightjar (*Caprimulgus ruficollis*), which also breeds in the Iberian Peninsula; and the distinctive Brown Nightjar (*Caprimulgus binotatus*). The last of these was once placed in its own genus *Veles*, and probably deserves to be returned there owing to its morphological differences from other

Caprimulgus species. These features include small "ear-tufts" at the rear of the head, slightly curved outer primaries, and stiff tail feathers which are held in an inverted "V" posture when the bird is at rest.

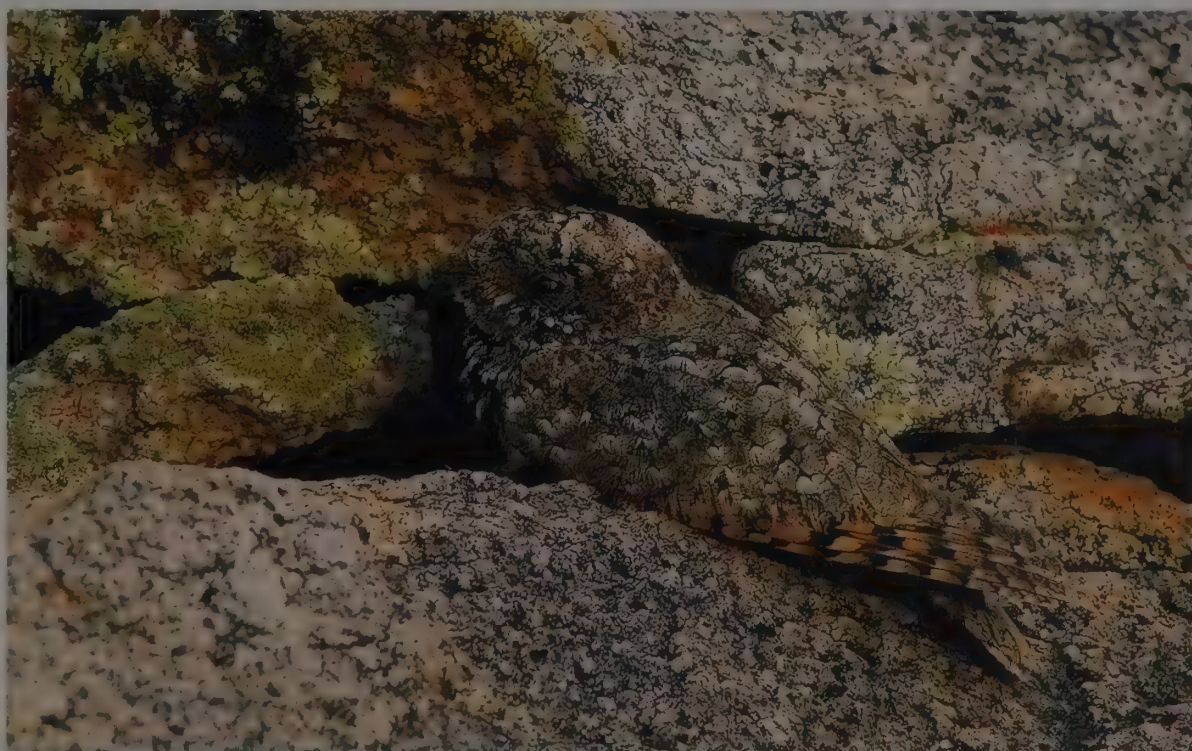
The two Madagascan endemics within this genus are the Collared Nightjar (*Caprimulgus enarratus*), a boldly marked species which regularly nests in epiphytic or free-standing ferns above ground level and may be worthy of further taxonomic study, and the fairly common Madagascar Nightjar (*Caprimulgus madagascariensis*), which looks and sounds remarkably similar to a widespread Asian species, the Indian Nightjar (*Caprimulgus asiaticus*).

The Common Poorwill occupies a monotypic genus, one peculiarity being that it regularly enters torpor in response to low temperatures and low food abundance, sometimes for long periods in a kind of hibernation during the non-breeding season. While dormant, or during daytime, its plumage defends it from the danger of predation, being perfectly adapted to blend in with rock and gravel in the deserts, plains and prairies of North America.

The Ladder-tailed Nightjar's plumage is patterned differently to protect this species while it roosts and nests on the sandbars and beaches exposed during the dry season along South American rivers. Roosting nightjars tend to flatten themselves when danger approaches, behaviour that results in a reduction of shadow and outline; also, they often close their eyes almost completely to increase their crypsis, appearing restful while actually remaining acutely alert.

[Above:
Phalaenoptilus nuttallii,
Arizona, USA.
Photo: John Shaw/
Auscape.

Below:
Hydropsalis climacocerca
climacocerca,
Manu National Park, Peru.
Photo: Günter Ziesler]



There are fewer *Caprimulgus* nightjars in Asia and only one superspecies grouping, the latter containing the Large-tailed (*Caprimulgus macrurus*), Jerdon's (*Caprimulgus atripennis*), the Philippine (*Caprimulgus manillensis*) and the Sulawesi Nightjars (*Caprimulgus celebensis*), all four having previously been regarded as conspecific. The ten subspecies of the widespread Savanna Nightjar (*Caprimulgus affinis*) are roughly split into seven southern, island forms and three larger northern forms, the latter having formerly been classified as a separate species called Franklin's Nightjar (*Caprimulgus monticolus*). There are three central Asian desert nightjars: Vaurie's Nightjar (*Caprimulgus centralasicus*), Sykes's Night-

jar (*Caprimulgus mahrattensis*) and the Asian population of the Egyptian Nightjar. Superficially, Sykes's and the Egyptian are very similar to look at, but because of their differing vocalizations and wing and tail markings they are not considered to be so closely related as to form a superspecies. Vaurie's Nightjar is certainly worthy of further study: it is still known only from the type specimen taken in 1929, although it remained misidentified as an Egyptian Nightjar for 31 years, eventually being described as a new species in 1960. Apart from the Indian and Salvadori's Nightjars, mentioned above, the two remaining Asian species are the Jungle Nightjar (*Caprimulgus indicus*), which is occasionally described as the



eastern counterpart of the European Nightjar, and the little-known Bonaparte's Nightjar (*Caprimulgus concretus*) of Sumatra, Borneo and Belitung Island.

The two highly distinctive *Macrodipteryx* species occur only in Africa. Although the Pennant-winged Nightjar (*Macrodipteryx vexillarius*) and the Standard-winged Nightjar (*Macrodipteryx longipennis*) are currently placed in the same genus, they are not thought to be sufficiently closely related to represent a superspecies, and indeed for many years taxonomists placed the Pennant-winged in its own genus, *Semeiophorus*.

The five remaining nightjars are all poorly known South American species. The Ladder-tailed (*Hydropsalis climacocerca*) and Scissor-tailed Nightjars appear to be related and share the same genus, while the Swallow-tailed (*Uropsalis segmentata*)

and Lyre-tailed Nightjars (*Uropsalis lyra*) share another. The rare Long-trained Nightjar (*Macropsalis forcipata*) is a monotypic species with its own genus.

One recent discovery has posed quite an interesting problem to taxonomists. During a 1990 survey of the Nechisar National Park in southern Ethiopia, remains of the decomposing corpse of a nightjar were encountered half-buried in a vehicle track in a treeless area. Tantalizingly for science, the tail feathers blew away while the remains were being freed from the soil, but a single wing was recovered in fair condition. Subsequent comparison of the wing with those of the four species known from the area showed it to be markedly larger. This called for the identification attempt to be transferred to the museum desks, where the wing was compared with skins of other large African nightjar species, and then of all other nightjar species available. After extensive examination, it emerged that this wing was amongst the most distinctive of any nightjar, in particular because of the positioning of the white primary patch unusually close to the carpal joint; it was not similar to that of any other species known. On this basis, the wing was used to describe the Nechisar Nightjar (*Caprimulgus solala*). Nevertheless, despite the extensive analysis and the undeniable distinctiveness of the wing, the validity of the species remains under question. A single wing seems rather a meagre sample to permit the definite conclusion that a distinct species is involved, especially as the differences, while notable within the context of nightjars, are not perhaps so very remarkable. Although the chances that this wing belonged to an aberrant individual are difficult to reconcile with the array of species that could potentially be involved, they can not be convincingly ruled out, so for the present the best course may be to delay its recognition as a valid species until more evidence is produced; this is the view adopted here. It is sometimes argued that recognizing a dubious form as a valid species can help promote interest in its conservation. However, in this case it may be that tentative rejection of this claimed species may actually act as a stronger spur for ornithologists to go out and try to prove beyond all doubt its existence as a valid species.

Morphological Aspects

Nightjars are generally medium-sized birds with fairly long wings, although they range in size from the Neotropical Least Nighthawk, which averages 15-19 cm in length and weighs less than 30 g, to the Great Eared-nightjar of Asia, which can measure up to 40 cm and weigh over 150 g. In addition, the males of

Although most nightjars rely on vocal communication to advertise for mates and defend territories, some species have evolved conspicuous visual signals which are used in display. The outer tail feathers of male Scissor-tailed Nightjars can reach 36 cm in length and thus protrude conspicuously beyond the remaining rectrices. This deeply forked tail is made obvious during courtship when stereotyped displays are performed on open patches of ground. Males extend their wings, then close them rapidly, making a small snapping sound and simultaneously hopping into the air.

[*Hydropsalis torquata fuscifera*, Cerro Corá National Park, Anambay, Paraguay. Photo: Robert Behrstock/VIREO]



The genus *Uropsalis* comprises two spectacular species largely restricted to the Andean cloudforests. One of these, the Lyre-tailed Nightjar, ranges from Venezuela to northern Argentina. During the breeding season males grow extremely long tail feathers which can reach some 75 cm in length. Several males often gather at communal leks, flicking these plumes to and fro when hovering, and calling in flight and pursuing females which visit the display ground.

[*Uropsalis lyra lyra*, La Soledad, Mérida, Venezuela. Photos: Robert Behrstock/VIREO]

Another species with sexually selected plumage modifications is the Pennant-winged Nightjar of sub-Saharan Africa, although in this case the elongated feathers are inner primaries rather than rectrices. These feathers are displayed by males at leks either in flight or on the ground. While individual males appear to hold territories within leks, they are not territorial at breeding sites and in many areas the species forms loose colonies with several nests only a few metres apart.

[*Macrodipteryx vexillarius*, near Bulawayo, Zimbabwe.
Photo: Brendan Ryan/Planet Earth]



several species can appear even larger in their breeding plumage. In the Neotropics, the males of a number of species have extremely long outermost tail feathers, which in the Lyre-tailed Nightjar can be up to about 75 cm long, while in the Afrotropics, the males of two species grow enormously elongated second primaries.

For their size, most nightjars appear to be reasonably large-headed, and yet, despite this, they have only a very small, weak-looking bill. They do, however, have an enormous gape, with an extremely sensitive palate, and are able to open their mouths both vertically and horizontally by using a highly specialized spreading mechanism of the lower jaw. In addition, their eyes are relatively large and situated laterally on the head. All these adaptations are, of course, advantageous to a nocturnal, aerial feeding strategy, but the skull consequently needs to be large enough to support these features. Nightjars have raised nostrils that are usually found along the top and towards the rear of the upper mandible, and in most species the gape is surrounded by extremely long, and possibly very tactile, rictal bristles, the exceptions being the nighthawks and the *Eurostopodus* nightjars. These bristles are actually strong, barbless contour feathers which are connected to special muscles in the skin, and are probably a further adaptation to nocturnal feeding. Evidence of another, possibly unique morphological feature in nightjars shows up only at night: this is the distinctive "eye-shine" that is noticeable when the birds are seen in artificial light. This is the result of light hitting a reflective surface called a tapetum, which is situated behind a layer of photoreceptors in the retina, at the back of the eye. A tapetum helps to increase the amount of light entering the eye and therefore improves vision at dusk and dawn and during moonlit nights, and is yet a further adaptation to nocturnal activities.

Nightjars are superb fliers and generally have long, slender wings with fairly pointed tips, although some species, such as the poorwills, have slightly shorter, broader and more rounded wings. A few species have evolved very unusual wing and tail structures which are used during courtship display flights (see Breeding). Male Pennant-winged and Standard-winged Nightjars of tropical Africa develop a greatly elongated pair of inner primaries, while male Sickie-winged Nightjars of South America have curved primaries and very short, almost non-existent-looking secondaries. Breeding males of five other South American species, the Ladder-tailed, Scissor-tailed, Long-trained, Swallow-tailed and Lyre-tailed Nightjars, possess unusually shaped and/or elongated outer tail feathers. Whatever their overall wing shape, all species are extremely agile in the air and obtain their high

degree of aerial skill through low wing-loading, which is achieved by having a very large wing area in proportion to body weight, and by having a highly manoeuvrable tail which serves as a perfect rudder.

Most nightjars have short tarsi and small, weak feet, which might suggest that they are uncomfortable on the ground. This is not, however, the case and many species can walk quite strongly, this being especially true of chicks. Some occasionally feed on the ground by picking up or even chasing insects. Species with rather longer tarsi include the Nacunda Nighthawk, the *Siphonorhis* poorwills and the Pauraque, which is quite at home on the ground and is often considered to be the most terrestrial of all nightjars. All members of the Caprimulgidae have partly webbed toes, with four phalanges in the outermost toe, two phalanges in the hallux, and a pectinate middle toe. The pecten is a small comb-like structure situated on the inner side of the claw and is possibly used for removing parasites, or straightening out the rictal bristles, during preening.

Adaptations to local environmental conditions take several forms. An important one for many nightjar species is the ability to withstand extremes of temperature. Nightjars are commonest in warmer climates and often roost and nest in open situations where they can be subjected to long periods of direct exposure to the sun. In these circumstances, they can keep cool by losing heat through gular fluttering, during which the mouth is opened, the gular area is vibrated, and the rate of blood flow to the buccal area is increased. Nightjars may also be able to maintain their brain temperature at a lower level than the rest of their body, by way of heat exchange through a highly vascularized region in the temples; this is certainly known to occur in one species, the Lesser Nighthawk.

Some nightjars also experience periods of cold weather, which affects not only their own level of activity but also that of their insect prey. At least some species have the physiological ability to lower their body temperature, reduce their rate of metabolism, and therefore become capable of entering and arousing from torpor. The first documented case of torpidity in nightjars is that of a Common Poorwill found in an apparent state of hibernation in the Chuckwalla Mountains of California, in December 1946, although naturalists may have been aware of torpidity in this species since the 1890's and native peoples probably knew of it even before then, the Hopi Indians' name for the bird being *Hölchko*, "the sleeping one". Since the late 1940's, investigations into the possible use of torpor by nightjars have been undertaken on both wild and captive birds of several species, including the Common Poorwill, the Common Nighthawk, the Whip-poor-will, the Eu-



During the breeding season, male Standard-winged Nightjars sport one of the most outlandish ornaments, not only within the Caprimulgidae, but of any bird. They possess highly modified second primaries, in this case consisting of a long bare shaft terminating in broad racquets. Both species in this African genus emit rapid high-pitched calls and they differ in their breeding biology from other nightjars studied. In particular, their mating system appears to be polygamous with several males attending display arenas that are visited by females. In the Standard-winged Nightjar, males circle potential mates while quivering stiffly bent wings in a slow undulating flight with their "standards" borne aloft. At rest, these bizarre feathers are held along the ground, perpendicular to the body. Despite considerable similarities, the two *Macrodipteryx* species are not thought to be particularly closely related because of discrepancies in plumage and wing shape.

[*Macrodipteryx longipennis*.]

Above: Garamba National Park, Zaire.
Photo: Marco Sacchi.

Below: Conakry, Guinea.
Photo: Dave Richards]



ropean Nightjar and the Spotted Nightjar, but it seems that the Common Poorwill is the only nightjar that regularly utilizes this physiological capability to counter periods of low temperatures and poor food availability. Studies suggest that the Common Poorwill may become dormant when its body temperature falls below about 20°C and, quite remarkably, it can lower its body temperature to below 5°C during torpor and fly with a body temperature as low as 27.4°C, both values being the lowest recorded in any species of wild bird. In parts of its range, it is also known to enter prolonged periods of torpor, often referred to as hibernation, to help it survive poor weather during the non-breeding season. Other species that occur in more northerly or southerly latitudes or breed at higher altitudes do not appear to enter torpor regularly during bad weather, and usually overcome the shortage of food resulting from cold winters by migrating to warmer climes.

Most species have highly variegated plumages, with the upperparts and breast usually a variable mixture of brown, grey, white, black, buff, tawny, rufous and cinnamon, broken up with brownish or blackish streaks, spots or vermiculations. Such complex plumage patterns are essential for camouflage at the roost- or nest-sites, and the overall coloration is usually an adaptation to the local soil or habitat type. The underparts, which are visible only when a bird is in flight, generally tend to be buffish or off-white, barred brown. In many species, males have large white markings on the wings, tail and throat, the most extreme example being the White-winged Nightjar of South America, which has largely white wings, except for the inner wing-coverts and black primary tips, and an almost entirely white tail. In some species, white markings are present in both sexes. These markings stand out as strong visible signals during territorial aggression, courtship displays, and defence and distraction displays at the nest-site, but they are tucked away and hidden from view when birds are roosting, incubating or brooding. Two species appear to lack all forms of white markings, these being the Bahian Nighthawk of the Neotropics and the Afrotropical Standard-winged Nightjar, while several others, including the Brown Nightjar and some of the *Eurostopodus* species, have only the white throat patches. At hatching, chicks are usually covered in a pale down, but they quickly grow their first set of feathers, after which they generally look fairly similar to the adults.

Most nightjar species replace their plumage in one annual, post-breeding moult, and many attain adult plumage during their first winter, although a few remain in immature plumage until their second winter. Juveniles of a few species have only two partial moults during their first winter, and they tend to keep

their "second-year" plumage until the following annual moult. A complete moult is not always undertaken in one go, and some migratory species suspend a moult started on the breeding grounds and complete it at the wintering sites. Generally speaking primary moult is descendant, secondary moult is ascendant and tail moult is centrifugal, although the outermost tail feather (T5) is often renewed before the adjacent T4. Not all nightjars, however, share the same moult pattern. Some species within the genera *Caprimulgus* and *Macrodipteryx* have a secondary moult that commences at the outermost and innermost feathers and converges in the centre of the inner wing; some *Caprimulgus* and *Eurostopodus* nightjars have a serially descendant secondary moult; and another *Caprimulgus* species replaces the outer secondaries ascendantly and the inner secondaries centrifugally. Male Pennant-winged Nightjars have an unusual wing shape; they replace their primaries in a generally descendant sequence, although P4-P2 are moulted ascendantly.

Habitat

The vast majority of species within the family Caprimulgidae are permanently distributed in warm climates around the globe, but in many other regions where there are seasonal periods of hot and cold weather nightjars will move in to breed during the summer and depart again to escape the winter. They spend much of their time on the ground and usually need plenty of broken cover in which they can roost or rear their offspring. They occur in all types of habitat from deserts to rain forests, but semi-open country with trees and bushes is possibly preferred throughout the entire range, and areas where there is at least some kind of surface water are frequently occupied.

Nightjars can be found at all altitudes from sea-level, where some occur on or near beaches and shorelines, up to about 4200 m. Species of the more mountainous regions include Archbold's Nightjar of New Guinea, and several species in South America, such as the Roraiman Nightjar which is endemic to the "tabletop" mountains of the Pantepui region of southern Venezuela and north-west Brazil, and the Andean trio comprising the Rufous-bellied Nighthawk, the Swallow-tailed Nightjar and the Lyre-tailed Nightjar.

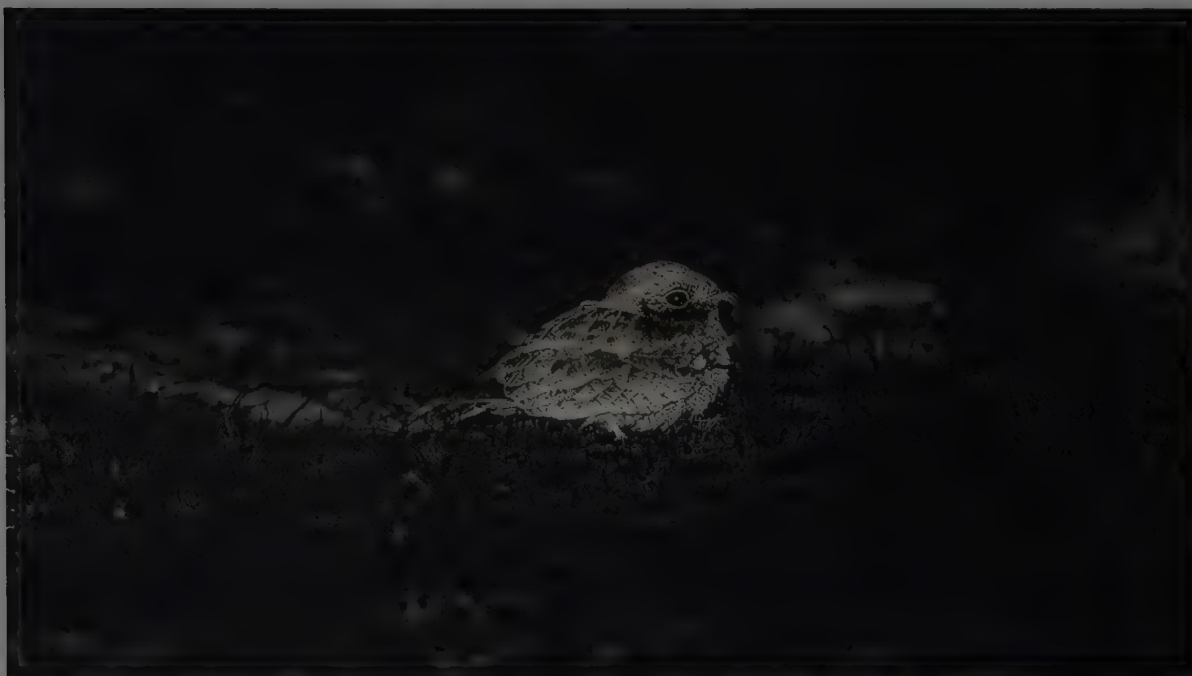
Deserts and semi-deserts with very little vegetation would appear to be among the poorest of places for nightjars, yet several species have adapted to living in the harsh conditions on offer there. These include the Egyptian Nightjar of Africa and



While the long wings and tiny feet of nightjars are indicative of their predominantly aerial habits, they roost and breed on the ground. Most nightjars frequent scrubby or bushy habitat, choosing open spaces in which to nest. Only a few species inhabit dense forests, nesting and roosting on leaf litter and generally feeding above the canopy.

Even within species, however, habitat choice is varied. The European Nightjar, for example, breeds on heaths and moorlands, young forestry plantations, chalk downland, scrubby steppes, stony hillsides, shingle banks, sand dunes and deserts, then spends the non-breeding season in the savannas, Acacia woodlands and highlands of Africa. It tends to avoid urban areas, mature forests, treeless plains and mountains, although it has been recorded up to 2800 m in the breeding range, and 5000 m in the Afrotropics.

[*Caprimulgus europaeus*
europaeus,
Hankley Common, Surrey,
England.
Photo: Melvin Grey/NHPA]



The Star-spotted Nightjar is locally common in parts of East Africa, notably Ethiopia and northern Kenya, frequenting stony grassland and black laval deserts. In appearance, it is quite similar to the Plain Nightjar (*Caprimulgus inornatus*), with which it is thought to form a superspecies. Although the breeding ranges of these two forms narrowly overlap, reproductive isolation is presumably maintained by their very different vocalizations.

[*Caprimulgus stellatus*,
Nechisar National Park,
Ethiopia.
Photo: Göran Ekström]

Asia, the Afrotropical Golden Nightjar, and possibly Vaurie's Nightjar of central Asia. Savannas and other grasslands, including areas with a composition nearer to that of a swamp or marsh, are inhabited by a few specialized nightjars; these include two extremely uncommon Neotropical species, the Sickle-winged and White-winged Nightjars, and the more widespread Afrotropical Swamp Nightjar. Species found in grasslands often seem to prefer areas where there are low structures such as bushes or termite mounds to perch on or to sing or display from. However, grasslands are often rather unstable environments which may be subjected to fires, flooding, trampling by large herbivores, or destruction for agricultural purposes, and the nightjars which live in them may frequently be forced to move to other regions.

Some species are often found in rocky or boulder-strewn terrain and at least two, the Neotropical Blackish Nightjar and the Afrotropical Freckled Nightjar, are known regularly to lay their eggs directly on rock surfaces. Other species, such as the Buff-collared Nightjar in Central America and Salvadori's Nightjar of Sumatra and Java, spend part of their time near cliffs, where they use the cliff faces to hunt from. In many regions, nightjars will frequent rivers and streams, and in South America species such as the Sand-coloured Nighthawk and the Ladder-tailed Nightjar are highly adapted to roosting and breeding on the sandbars and riverbanks exposed by low water levels during the dry season. Many of the world's nightjars, however, especially *Caprimulgus* species, actually occur in a wide variety of habitats and are often found in regions with a mixture of open ground, grassland, bushes, shrubs and trees. Others have taken to woodland and forests, where they prefer clearings and openings, the edges of roads, tracks or paths, or the borders and edges of the woodlands themselves.

As a general rule, nightjars tend to shy away from man-made habitats and usually avoid large urban areas, dense stands of forestry, agricultural country with few trees and little or no ground cover, and intensively farmed regions. A few species, however, will always exploit new opportunities as they arise, and some are frequently encountered in seemingly alien environments. Artificial lights, animal corrals or concentrations of livestock often attract large numbers of insects at night, and hunting nightjars soon learn to take advantage of such localized food sources. In North America, the Common Nighthawk is certainly not afraid of towns and cities and regularly nests on flat, gravel-topped roofs in some areas, frequently catching moths and other insects attracted to the light of street lamps. Roof-nesting has also been recorded for species in South America, Europe, Asia and Africa, albeit on a much smaller scale than in the Common Nighthawk.

Migratory species, which can cover huge distances between their breeding and wintering grounds, are always likely to turn up in atypical situations, often as a result of exhaustion or disorientation.

General Habits

Nightjars are secretive, nocturnal birds which are most active at dusk and dawn and during periods of strong moonlight, although a few species, such as the Common, Lesser and Antillean Nighthawks, can be equally alert at certain times during the day. Most species tend to leave their roost-sites at or during the twilight period of dusk, although during dull and overcast weather conditions many birds can often be seen slightly earlier, while others are more nocturnal and do not become active until well after dark. At certain times, especially when there is plenty of moonlight or when there are chicks to be fed, they can also be active throughout much of the night. They almost always return to their roosts before dawn.

Most nightjars usually roost on leaf litter on the ground, but they will also rest on bare soil, sand, pine needles, rocks, boulders, tree stumps, logs, roots and branches in trees. Some birds occasionally roost on artificial surfaces such as the roofs of buildings, or on man-made materials on the ground such as cardboard or sacking. Whatever site is chosen, it is usually somewhere where they can use their cryptic plumage to blend in with their surroundings and where they have a good view of any approaching danger. Nightjars tend to have several favoured roost-sites within their home range and will often use one site day after day, but they nearly always change sites once they have been disturbed. Nightjars often roost alone, although pair-members occasionally roost together, and in some regions, especially during the non-breeding season, many species often roost semi-colonially at favoured sites.

Roosting nightjars often awaken for short periods during the day, and they will then sit upright, preen, stretch their wings or gape widely, an action which looks remarkably like a big yawn! They may also move short distances, especially if they have been roosting in direct sunlight for too long, move around to face the sun, thereby reducing their tell-tale shadow, or move away from cooler, shaded spots to sunbathe. If danger approaches, a roosting bird immediately assumes a "vanishing" posture by slowly flattening itself to the ground, lowering its neck, head and bill, and closing its eyes until they are almost fully shut. While in such a position, nightjars are extremely alert and actually keep

The Collared Nightjar, one of two members of the family found on Madagascar, is a scarce bird largely restricted to the eastern humid forests. Its taxonomic placement perhaps deserves further study, since its bold, distinctive markings and unusual behaviour suggest that it might belong in a separate genus. Although it generally prefers denser, more continuous forest than most nightjars, it has also recently been discovered inhabiting brush and mangroves in the west. Individuals hawk for insects, either above or below the canopy, and have been recorded sallying repeatedly from emergent bare branches. It appears to be oddly silent for a nightjar and no song has ever been described, a circumstance which exacerbates the considerable difficulty of locating the species. It is most easily encountered in some of the better known protected areas, such as the Perinet-Analamazaotra Special Reserve, where regular roosting sites are known by local guides. Although it sometimes breeds on the ground, nests are also positioned fairly high in epiphytic or free-standing ferns. This behaviour is presumably an adaptive response to high predation rates, although in Madagascan forests snakes appear to be the only potential egg thieves sufficiently abundant to produce this effect.

[*Caprimulgus enarratus*,
Perinet-Analamazaotra
Special Reserve,
Madagascar.
Photo: Nick Garbutt/
Planet Earth]





The Nacunda Nighthawk is a large Neotropical species that occupies a monotypic genus. It spends much time on the ground, often walking upright and standing rather than sitting on relatively long, robust legs, in comparison with the tiny tarsi and feeble feet of most nightjars. Like several other nighthawk species, it is partially diurnal, regularly gathering in large feeding or migrating flocks high over open country. It is a summer visitor to southern portions of its range, occasionally straggling to Patagonia in the austral summer.

[*Podager nacunda nacunda*,
Açurizal Reserve,
Pantanal, Brazil.
Photo: Günter Ziesler]

watch on whatever is going on around them, through the tiniest of slits between their eyelids. Should the potential threat approach too closely, a roosting nightjar immediately takes flight, flies away from the roost-site and quickly re-alights, where it either remains alert or once again adopts the flattened posture. If detected, nightjars flushed from their roost during the day are frequently mobbed by other birds, possibly because of their resemblance in shape to small birds of prey or parasitic cuckoos, and they are then at risk from predators such as hawks or falcons. If seen at dusk, nightjars leaving their roost also attract attention from other birds, or even bats, and may be preyed upon by larger species of owl.

Nightjars are mainly aerial feeders (see Food and Feeding) that carry out most of their hunting during their main activity periods at dusk and just before dawn. Normally, they have several relatively inactive spells during the night, and often sit on roads, tracks or paths or in other open spaces, or, in the case of some species, perch high up in trees. They sometimes hunt from these resting places, usually by making short flycatching sallies after passing insects, but quite often they will just rest or preen. While preening, nightjars maintain and waterproof their plumage, using the bill to transfer oils from down feathers on the breast and above the tail; the uropygial gland tends to be rather small. Some species occasionally dust-bathe, although such behaviour is poorly documented.

They often drink water, preferring to take it from the surfaces of lakes, ponds and slow-moving rivers rather than from fast-flowing waterways. Some species will also drink from artificial sites such as cattle troughs and swimming pools, especially in regions with very limited or no natural water supply. They usually drink in flight, normally by gliding low over the water surface with their wings and tail held up, and either "trawling" with an open bill or repeatedly dipping the bill into the water. Another, more hesitant, approach is to descend to the water in a series of short hovers before drinking and flying off. Some species, such as the Lesser Nighthawk, will also alight at the water's edge and drink with a "bobbing" action of the head and neck.

As a rule, these are highly inquisitive birds. They will often investigate intruders within their territory by approaching fairly closely and hovering nearby, although potential predators such as owls, foxes, cats and snakes are frequently mobbed or chased. Males holding territory are also fairly aggressive towards other

males of their own species, and will harass or even fight intruders to drive them away; such behaviour is usually commoner at the beginning of the breeding season.

Nightjars remain among the most poorly known of all birds and are difficult to observe, yet radio-tracking studies and the use of image-intensifying equipment are beginning to reveal some secrets of the behaviour of at least a few species.

Voice

Although nightjars generally seem to be rather silent, mysterious birds, they actually have quite a large repertoire of calls and can be particularly vocal at certain times, especially during the early part of the breeding season. On the other hand, they are often silent for much of the rest of the year. The main vocalizations of all species appear to be the advertising calls or "songs" of the males, which are given from a perch, in flight, or from the ground. Some species also make mechanical, clapping or "booming" sounds with their wings (see Breeding).

The most obvious sound given by the majority of species is the main advertising call of the male, which usually serves to proclaim a breeding territory and attract a mate. Although such calls play a vital role in the life cycles of all species of birds, they are especially important to nightjars, as nearly all of their main activities take place at night. Males often choose to "sing" or call from an elevated perch such as a tree branch, fence post, overhead wire, rooftop or boulder, but some sing or call in flight, often high above the ground, and some sing from the ground itself. Nightjars appear to sing with their bill closed, and project their calls in different directions either by turning about on one song-perch or by flying around their territory and calling from different places.

Advertising calls can carry a long way but are less audible in bad weather, and nightjars are often silent or sing only briefly in adverse conditions. Peak calling times for most species are dusk and dawn, although nightjars often sing throughout the night when there is plenty of moonlight. They tend to sing more strongly prior to and at the beginning of the breeding season, and sing much less often once a pair-bond has been formed or the eggs have been laid. Some species, such as the Common Nighthawk,

Despite the proximity of Madagascar to the African mainland, there are many clear links between the Malagasy and Asian avifaunas. It is thus less surprising that the Madagascar Nightjar, endemic to the Indian Ocean islands, looks and sounds remarkably like the Indian Nightjar (*Caprimulgus asiaticus*). Like most nightjar species it possesses elongated and extremely tactile rictal bristles around the bill.

These feathers are attached to special muscles in the skin and are presumably related to its nocturnal feeding habits. It is the commonest nightbird in Madagascar, occurring in almost all habitats on the island except humid forest where it is replaced by the Collared Nightjar (*Caprimulgus enarratus*).

It frequents lighter woodland, plantations, cultivation and even urban areas where it has been recorded nesting on the roofs of buildings. The densest populations, however, are found in the spiny forests of the south and south-west, a distinctive dry habitat characterized by baobabs and strange *Didierea* trees. In this area, large numbers congregate after rain to feast on dispersing termites, and they frequently fly out over the sea at dusk, feeding on flying insects low over the Mozambique Channel.

[*Caprimulgus madagascariensis*, Berenty Reserve, Madagascar.

Photo: Daniel Heuclin/
NHPA]





All nightjars are agile and buoyant fliers, primarily because of the very large wing area in relation to their body weight, and skillful adjustments to the spread and angle of the tail which acts as a rudder in flight. This manoeuvrability allows them to pursue and capture highly mobile flying insects. The Nacunda Nighthawk has more rounded wings than most nightjars and its flight action is noticeably looser and more erratic. It is sexually dimorphic, the female having a less extensive area of white at the base of the primaries and more brown bars on the belly. The white patches on the wing and throat form conspicuous visual signals and are present in many nightjar species.

[*Podager nacunda*
nacunda,
Pantanal, Brazil.
Photo: Roland Seitre/Bios]

frequently give their advertising call during the day, and even some of the most nocturnal species may sing briefly if disturbed from their daytime roost.

Many species have large white throat patches, which are generally hidden by the surrounding throat feathers when a bird is roosting or at the nest-site. When singing, however, these patches are prominently displayed and are puffed out at each call note, and at close range they serve as a visual signal to potential mates or competing males. The females of some species are also thought to give similar calls to the advertising calls of their mates, although the exact reason for this has yet to be identified.

Several different groups of advertising calls are recognizable within the Caprimulgidae, the most remarkable being the monotonous sounds that are often referred to as "churring" and which are produced by repeating a long series of often identical notes very rapidly. Although it was this eerie sound emanating from the undergrowth at dusk that gave these birds their English name, such calls are in fact given by only a handful of *Caprimulgus* species in Europe, Africa and Asia. The "churrs" vary from long, evenly pitched series to others that vary in pitch or are interspersed with other call notes. One Neotropical *Chordeiles* species, the Lesser Nighthawk, has a song that could be interpreted as a slow churr, although it is more often referred to as a trill, and this gave rise to its alternative English name, the Trilling Nighthawk.

Perhaps the commonest types of nightjar advertising calls are the whistled forms, which are probably given by the majority of species. Whistled songs vary greatly and may be rather simple, such as those given by some of the *Nyctiphrynus* poorwills or certain *Caprimulgus* species such as the Band-winged Nightjar or the White-tailed Nightjar. At the other end of the scale, whistled songs may be more complex, and range from those given by species such as the Chuck-will's-widow and the Whip-poor-will, which appear to sing their own names, to the more musical whistles of species such as the Fiery-necked and Abyssinian Nightjars.

Other varieties of advertising call include those which resemble repeated knocking sounds, as given by species such as the Red-necked, Large-tailed and Swamp Nightjars; those which sound like a ball bouncing on a hard surface, as given by the Indian, Madagascar and Sulawesi Nightjars; and high-pitched, insect-like

or bat-like twitterings, as given by the two *Macrodipteryx* species, the spectacular Standard-winged and Pennant-winged Nightjars of the Afrotropics. At least two species of *Eurostopodus* nightjar, the Spotted and the White-throated Nightjars of Australasia, have songs consisting of a series of "bubbling" notes.

Many species also have distinct flight calls which differ significantly from the main advertising call and are often given at times of contact with other birds of the same species. Contact calls vary greatly between species but often consist of clucking, croaking, chattering, twittering or whistling sounds. Nightjars utter a variety of other calls at all stages of their life cycle, especially at the nest-site, these ranging from soft murmurings, cooings and single call notes to churrs, rattles, squeaks, nasal "pinks" and throaty hisses. Chicks frequently make soft peeping or cheeping sounds, although they immediately become silent at the first sign of danger.

The most striking of all calls given by nightjars is a loud, guttural hissing sound that slowly rises in pitch and volume as the huge gape is opened. Such calls are always given in circumstances when the individual bird feels threatened, and similar sounds appear to be common to all members of the family in the same situations. Although usually uttered during defence or distraction displays at the nest-site, where they are intended to frighten off potential predators, they are also frequently given when a nightjar is handled by humans. Feathered, unfledged chicks will also emit this sound when cornered.

Food and Feeding

Nightjars are generally insectivorous feeders that hunt by sight and take a wide variety of prey. Their food is composed mostly of night-flying, winged insects which are captured and swallowed in flight, although many species also take insects from surfaces such as leaves, branches and logs, and some occasionally take prey items from the ground. This diet has enabled the family to occupy a wide range of habitats, and feeding nightjars have few competitors apart from bats.

Details of the dietary requirements and foraging behaviour of the Caprimulgidae are available for only a few well-studied species, such as the European Nightjar and the Common

The Sand-coloured Nighthawk is probably the most diurnal and gregarious of all nightjar species. It is highly adapted to riparian habitats in the Amazon basin, sometimes occurring near villages and clearings in forest but rarely straying far from water. While other nightjars tend to be encountered as solitary individuals or pairs, this species feeds, roosts and nests communally, usually on riverbanks and sandbars beyond the reach of most terrestrial predators. Flocks of up to 50 individuals are regularly observed foraging over rivers while colonies of more than 200 pairs have been recorded, often adjacent to nesting groups of Black Skimmers (*Rynchops niger*), Large-billed Terns (*Phaetusa simplex*) and Yellow-billed Terns (*Sterna supercilialis*). Males display near the colonies, walking towards females then stretching horizontally with wings raised to reveal the conspicuous underwing pattern. Their eggs or chicks are predated by a variety of raptors and are often harvested by local people as a seasonal supplement to the local protein intake.

[*Chordeiles rupestris*
rupestris,
Manu River, Peru.

Above:
Herbert Clarke.

Below:
Patricio Robles Gil/
Sierra Madre]



Nighthawk. Most of the information on food taken by the members of this family comes from the analysis of stomach contents, either from birds taken for museum specimens or from road casualties. Prey items range in size from the smallest of gnats and mosquitoes to fairly large hawkmoths and locusts, although larger insects are presumably easier to hunt visually and are more beneficial in terms of nutrition gained to energy expended. On the wing, nightjars usually take numerous moths, beetles, flies, mantids, bugs, cicadas, lacewings, caddisflies, mayflies, damselflies, dragonflies, winged termites and ants, wasps, mosquitoes, gnats, cockroaches, grasshoppers, locusts, crickets and occasionally butterflies. Prey items taken from leaves, branches or the ground include flightless glow-worms, moth larvae, locust nymphs, caterpillars, small bivalves, earwigs and spiders, while insect egg cocoons, mites, small pieces of wood and vegetation, small seeds, earth and grains of sand are also ingested, in some cases no doubt accidentally. Gravel, grit, pebbles and stones are also swallowed, sometimes deliberately, and possibly aid the breaking-up of indigestible animal matter, which is later regurgitated in pellets. In Asia, the food of the Indian Nightjar in winter is documented as including *Euphorbia caducifolia* flowers and small mice (*Mus cervicolor*), while in North and Central America the Chuck-will's-widow is known to take small birds such as hummingbirds, swallows, warblers (Parulidae) and sparrows (Emberizidae).

Most species forage mainly at dusk and dawn, and their extremely agile and buoyant flight is constantly interrupted by sudden twists, turns, wheels, rises and descents as they spot and chase after prey. With such wide gapes, nightjars are often thought to trawl for insects by flying around with their mouths open, especially as prey items as small as mosquitoes are often taken, but generally they just snap at insects when they come within range. Most nightjars also have elongated rictal bristles around their gapes, and these sensitive, modified feathers probably help to locate or funnel insects into the mouth. Between chases, they frequently glide around with their wings held in a "V" shape above their body. While hunting, some nightjars also occasion-

ally hover and swoop down after prey. Some species, such as the *Chordeiles* nighthawks, often hunt in a faster, even more erratic flight that is also interspersed with short glides. Nightjars occasionally forage during daylight, especially in very overcast conditions, although such behaviour usually takes place just before dusk or just after dawn.

Hunting nightjars will usually take food in the air space between ground level and above treetop height, although some species, such as some of the larger nighthawks, often forage very high up at about 150-175 m above ground. Nightjars usually forage alone, but in many regions, especially during migration periods and the non-breeding season, up to 20 or more birds of more than one species have been recorded gathering at good food sources, such as around grazing animals, animal corrals, lights or fires, or at insect swarms or termite emergences. Some species of nighthawk, such as the Common and Lesser Nighthawks, often forage in large flocks of several hundred birds.

Later in the night, when there is less available light than at dusk or dawn, nightjars sometimes change their foraging strategy to a wait-and-see technique, by flycatching from a perch or from the ground. During this method of hunting, a nightjar leaves its perch when an insect comes within range, pursues it in a short, acrobatic flight and then returns to either the same or a nearby perch. Flycatching nightjars possibly use moonlight or the night sky to backlight their prey when it is too dark for prolonged aerial foraging. Species that occasionally take insects from foliage or branches do so by hovering briefly, plucking off the prey item in the bill and then flying off.

Nightjars feed on the ground by running and darting after food, although such behaviour is possibly not common in the majority of species. For a few species, however, ground feeding can be quite important at certain times of the year. The Chuck-will's-widow, for instance, undergoes a rapid moult on the breeding grounds, during which it is often unable to fly strongly, and the ability to hunt prey on the ground is obviously a valuable survival asset at this time. The Pauraque has relatively long tarsi, suggesting that it is more strongly adapted to a terrestrial life



The Rufous-cheeked Nightjar is an intra-African migrant, breeding in southern regions, including South Africa, Zimbabwe, Angola and Namibia, and spending the non-breeding season in West Africa, with the majority of birds visiting Cameroon and Nigeria during the austral winter. During courtship in September and October, males clap their wings in display flights over wooded savannas, Acacia scrubland and the sparsely vegetated semi-deserts of the Karoo, Kalahari and Namib. The species is closely related to the Sombre Nightjar (*Caprimulgus fraenatus*) of north-east Africa with which it was previously considered conspecific.

[*Caprimulgus rufigena* rufigena, Brandvlei, Northern Cape, South Africa.
Photo: Peter Steyn/Ardea]

The genus *Eurostopodus* contains seven species that are often termed the "eared-nightjars", although only two of them possess elongated superciliary tufts. They differ from most other members of Caprimulgidae in lacking prominent rectal bristles and any traces of white in the tail, and recent genetic research reveals that they might belong in a separate sister family, the *Eurostopodidae*.

Continued study might well support the further division of this new family into three genera as there is considerable variation in morphology, ecology and vocalizations within the group. The nominate race of the White-throated Nightjar usually breeds in dry forest, heathland or the fringes of humid forest in Australia, with southern populations wintering as far north as New Guinea. The dark Solomon Islands race *nigripennis* nests on or near beaches, while the New Caledonian form *exul* is known from only one specimen taken in lowland Melaleuca woodland in 1941. It has not been recorded since despite considerable efforts to locate it. Both *exul* and *nigripennis* are highly divergent from *mystacalis* and might prove to justify recognition as separate species, in which case they would both be considered threatened. Nest defence, at least in the nominate subspecies and many other nightjars, takes the form of a threat display during which the adult stands upright, stretches its neck and wings and spreads its tail. This sometimes develops into a distraction display wherein the adult either hisses and retreats slowly or flutters to feign injury.

[*Eurostopodus mystacalis*
mystacalis,
Atherton Tableland,
northern Queensland,
Australia.
Photo: Clifford and
Dawn Frith]





All nightjars have very small, weak bills and yet their gape is enormous due to a highly specialized spreading mechanism of the lower jaw which means that they can open their mouths both vertically and horizontally. This adaptation, along with the extreme sensitivity of their palate, presumably enables them to catch and consume large or mobile insects in flight. Most species, including the Red-necked Nightjar, also use this broad gape to frighten intruders during threat displays at the nest. While raising their wings and gaping they emit curious guttural hissing sounds.

[*Caprimulgus ruficollis ruficollis*, near Páncas, Tagus Estuary, Portugal. Photo: Tony Tilford/Oxford Scientific Films]

style than other nightjars, as may also be the case of the *Siphonorhis* poorwills, though unfortunately ground-feeding by all three of these species is very poorly documented.

During the non-breeding season, many species can have rather a large home range in which to forage, but breeding territories are often smaller, and it has been found that nightjars sometimes travel distances of up to 10-15 km outside the territory to feed in areas with plenty of food. They will also drink when water is available (see General Habits).

In British Columbia, Canada, several recent studies have revealed that Common Nighthawks, when foraging, can fly at speeds of up to 5.3 m per second, pursue up to 18-19 items of prey per minute, capture more than one insect at a time, and spend up to 5.3% of each 24-hour period foraging. Studies of the Whip-poor-will, also in Canada, have shown that this species is generally lunarphilic, its activities and bouts of foraging being most intense during periods of twilight and bright moonlight, and it is highly probable that this also applies to most nightjar species. The same study in Canada also suggests that, although many insects are lunarphobic, being less active during twilight and in bright moonlight, the higher levels of light available during these periods probably help a foraging Whip-poor-will and provide an opportunity for a greater capture rate, despite there being less prey available. Studies of European Nightjars have demonstrated that while foraging they can take up to 12 prey items per minute, but if hunting using the flycatching technique they may make up to 28 sallies over a 15-minute period and pursue up to 31 items of prey.

Breeding

The ecology of nocturnal birds is difficult to study, and the breeding behaviour of almost all nightjar species remains little known and poorly documented. With a few exceptions, nightjars are

generally territorial, ground-nesting birds that have a monogamous breeding strategy, with pairs mating for life, or breeding together for one season only, or occasionally even changing partners between first and second clutches. In the majority of species, breeding pairs usually nest by themselves within their own territories, but some species occasionally breed semi-colonially, while a few sometimes nest in colonies. In some regions, breeding appears to be linked to particular phases of the moon, while in others it is influenced by the annual rains. Both sexes take active roles in parental care, although females usually spend more time at the nest-site during the day. The two Afrotropical *Macrodipteryx* species, the Standard-winged and the Pennant-winged Nightjars, have a different breeding strategy from that of other nightjars and are possibly polygamous.

The breeding cycle usually commences with males establishing a territory, which they do by "singing" from different points around an invisible boundary. Once a territory has been occupied, males generally defend it vigorously against other males, especially during the early part of the breeding season or before a pair-bond has been formed. The most common form of territorial defence is for a male to sing strongly towards a neighbouring singing male. Should two singing males be within visual range of each other, they may adopt an aggressive posture with their wings drooped and their tail fanned or raised in the air. The more extreme confrontations at territorial disputes involve physical contact, in which two males fly at each other while hitting out with their wings and bill-grappling. Fights of this sort can actually take place either on perches or in the air, and may end with both birds falling to the ground before they break off and go their own ways. Territory size varies from species to species and also depends on the amount of suitable habitat available to the local population. The smallest territories measure less than 1 ha in size, while the largest cover up to 40 ha or more, and, with habitat often dictating population densities in many areas, terri-



Nightjars often glide with their wings held in a distinctive "V" shape, a posture that they adopt when drinking in flight. This behaviour is perfectly illustrated by this series of photographs of a Common Nighthawk gliding low over the surface of a lake and "trawling" for water with an open bill. Although not the only technique employed by nightjars to drink, this is the most frequently recorded. They have also been observed dipping the bill repeatedly while hovering over water, or perching beside a water source and sipping at the surface. Nightjars tend also to bathe in flight, often using wind-driven rain which they fly towards then suddenly spread their tail, an action which stalls them in the air and pulls the body upright. They maintain this position with bouts of rapid fluttering while ruffling their rain-rinsed feathers. Common Nighthawks are indeed common over much of North America, migrating to South America in the non-breeding season, sometimes reaching as far south as Patagonia. They forage high over open country or water, occasionally in flocks of up to 300 individuals. Long-distance migration renders them prone to vagrancy and they are regularly recorded on the western seaboard of Europe in autumn after displaced individuals have inadvertently crossed the Atlantic.

[*Chordeiles minor*,
Texas, USA.
Photos: Tom Vezo]



Nightjars do not construct a nest as such, merely laying the clutch onto bare patches of ground, sometimes directly onto rock. The eggs tend to be whitish with a variable amount of brown, red or grey speckling. Traditional nesting sites are sometimes used year after year and most species nest alone in territories extending up to 40 ha. The Common Nighthawk generally follows this rule, but occasionally breeds in loose colonies, sometimes together with congeners. While nests of this species are most frequently placed in open country or woodland they have been recorded in the old nests of American Robins (*Turdus migratorius*) and on top of fence posts. Increasingly, man-modified environments are used too, such as the roofs of buildings or between the rails of railway tracks, incubating females apparently tolerating the trains regularly passing overhead.

[*Chordeiles minor*,
USA.

Photo: Kenneth W. Fink]

territories may be either far apart, side by side, or with boundaries that overlap in places.

Singing is also used to attract potential mates into the male's territory, and, once this has been achieved, males usually display to the females to try to establish a pair-bond prior to breeding. During courtship displays, the males of many species show off a series of prominent white markings on the throat, wings or tail (see Morphological Aspects), while some, such as those in the genera *Macrodipteryx*, *Hydropsalis*, *Uropsalis* and *Macropsalis*, deploy elaborate or elongated wing or tail feathers. Courtship rituals may be performed on the ground or on a perch, but more commonly they take place in the air.

During aerial courtship displays, some species, and especially the *Caprimulgus* nightjars, display their white markings during a gliding or "sailing" flight, with the wings held in a "V" shape above the body and the tail fanned at an angle. Many species, again notably male *Caprimulgus* nightjars, are also known to produce clapping or "whip-cracking" sounds with their wings. Common and Antillean Nighthawks display by circling high up, then diving through the air with their wings held in a "V" shape above the back. As they come out of the dive, they suddenly bend their wings downwards and produce a "booming" sound. A few species make other types of "mechanical" wing noise during their display flights: these include the Standard-winged Nightjar, which makes "frp" sounds, the White-winged Nightjar, which produces "frt" and short "tk" sounds, and the Sickle-winged Nightjar, which gives audible flaps and muffled "tuc" sounds.

The courtship of the Lyre-tailed Nightjar often takes place at communal display sites or leks, with several males calling and pursuing several females. Males also hover and move their elongated tail feathers to and fro. Male Long-trained Nightjars also display their enormously long tail feathers while courting females. They may display either from the ground, raising the tail to form a large white "V", or in flight, when the tail is fanned into an

inverted "V". Male White-winged and Sickle-winged Nightjars perform display flights around their territories by fluttering and gliding between exposed perches such as termite mounds, during which they use their uniquely shaped wings to produce the far-carrying mechanical sounds mentioned above.

Some courtship displays commence on the ground, with a male taking flight, circling and fluttering around the female, then alighting again nearby. During these short courtship flights, males often fly with their wings held level and rapidly quiver their wingtips. In the ground display of the Sand-coloured Nighthawk, the male stretches up, inflates his throat, fans his tail, sways from side to side and walks towards the female, before suddenly stretching horizontally, touching the ground with his inflated throat, and raising his wings to show off the underwing pattern. Male Scissor-tailed Nightjars often perform their courtship displays from open patches of ground, during which they stretch up their wings, suddenly close them to produce a snapping sound, and make little jumps into the air. Other displays, such as those given by the Puerto Rican Nightjar, often take place on tree branches or other elevated perches and often begin with a male and a female sitting parallel about 50 cm apart. The male may sing briefly while vibrating his body, drooping his wings and fanning his tail, then walk slowly towards the female. Copulation often follows a successful display. At the start of the breeding season, the males of many species usually roost alone within their territories. However, pair-members often roost together at the chosen nest-site prior to egg-laying, and once breeding is under way the male occasionally roosts close to the incubating female.

The two Afrotropical *Macrodipteryx* species both have display arenas, at which usually several males display to several females. The male Standard-winged Nightjar has a slow, undulating display flight during which he vibrates his stiffly bent wings, while his elongated second primaries, the flag-like "standards", float above and behind him. Pennant-winged Nightjars have two

types of courtship display. During their aerial displays, males glide around, often at treetop height, with their elongated second primaries, the "pennants", fluttering behind them, and are often followed by one or more females. For their other type of display, males alight on regular perches such as stones, termite mounds or even the ground, spread their wings and slowly circle around on the spot while vibrating their "pennants".

Nightjars usually prefer dry, open areas for nesting, and often choose nest-sites that are near or among vegetation, rocks, stones, logs or fallen branches, which typically offer some protection against the elements or predators. They do not build nests, and generally lay their eggs on leaf litter on the ground, or on bare soil, gravel or sand. Nightjars are often considered to make little scrapes in which to lay their eggs, but it is more likely that the small depressions which develop at the nest-site are caused by sitting birds and by the adults dislodging debris during change-over duties. Some species, such as the Freckled Nightjar and the Blackish Nightjar, frequently choose to nest on rocks or boulders, and lay their eggs on a thin covering of lichens, or on leaf litter or directly on the rock surface. The Semi-collared Nighthawk of South America may be unique among nightjars in that it nests in trees, laying its single egg in a branch hollow or at a fork. Two forest species for which few data are available are also thought to nest off the ground, at least on some occasions: the Brown Nightjar may lay its eggs on a palm frond, while the Collared Nightjar of Madagascar is known to nest in epiphytic ferns on tree trunks, or in the crowns of free-standing ferns, where the nest-site may be up to 1.5 m above ground. Nesting on the roofs of buildings is also well known and has been recorded for several species, including the Common Nighthawk and the Band-winged and Madagascar Nightjars, in different parts of the world. For the Common Nighthawk this is a common practice, and birds have been breeding on flat, gravel roofs in some urban areas of North America since at least the middle of the nineteenth century. Colonial nesters include the Sand-coloured Nighthawk, with up to 200 pairs often breeding close to each other on beaches and sandbars. Beach-nesting nightjars and nighthawks often lay their eggs close to the nests of other birds such as plovers (Charadriidae),

terns (Sternidae) and skimmers (Rynchopidae). Semi-colonial nesting is occasionally recorded, notably in the mixed-species associations of Common and Antillean Nighthawks. Some nightjars use the same favoured nest-sites year after year.

Nightjars generally lay clutches of only one or two eggs. Although three or four eggs have been recorded for a few species, such as the European Nightjar, these occurrences are extremely rare and are possibly the result of two females laying at the same site. In most species, the eggs are laid at intervals of 24-48 hours. Egg size ranges from about 22 x 17 mm in the Least Nighthawk to about 44 x 31 mm in the Great Eared-nightjar. Eggs are generally elliptical, smooth and whitish, although some species such as the Pauraque and the Papuan Nightjar often lay eggs with a pinkish or brownish ground colour. Markings of spots, blotches, freckles and scrawls may be blackish, greyish, brownish, reddish or lilac in colour, and eggs range from being completely unmarked to densely patterned, the latter especially at the fatter end. Having pale eggs enables a parent bird to locate them more easily at night, but the light colour may prove to attract predators during the day. Nightjars counter this, however, by sitting very tightly during the incubation period. Most species tend to be single- or double-brooded, although when conditions are favourable in tropical regions some may attempt to rear three broods in one season.

Eggs that are accidentally dislodged from the "nest" are occasionally moved back by the adult pushing them with its bill, but reports of nightjars deliberately carrying their eggs away from danger appear to be erroneous. After the eggs have hatched, however, pieces of eggshell may occasionally become stuck to the adults' legs or underparts, presumably with dried albumen, and this may give the appearance of eggs being carried.

The incubation period averages about 16-22 days in most species, the eggs hatching asynchronously. Chicks are covered in greyish, brownish, buffish or reddish down. Although fairly mobile from hatching, downy chicks are less cryptically coloured than their parents, and until the first set of feathers is grown they rely on the tight brooding behaviour of the adults for their protection. Although some chicks remain in the vicinity of the nest-

The Fiery-necked Nightjar inhabits the miombo and mopane woodlands of eastern Africa where it is locally common.

Like other nightjars, it does not make a nest, laying its eggs directly onto leaf litter amongst which the incubating adult is well camouflaged.

Like most nightjars it is often encountered sitting at night on the sandy roads that traverse its favoured habitat, easily picked out in car headlights at long range, due the glaring orange eye-shine.

[*Caprimulgus pectoralis fervidus*, north of Harare, Zimbabwe.
Photo: A. S. Weaving/
Ardea]





This Philippine Nightjar is only a few days old and its juvenile plumage has only recently started to emerge on its wings. Nightjar chicks are semi-precocial, being fairly mobile immediately after hatching, and covered in dense grey, brown or buffy down. As they are particularly vulnerable to predation at this stage, and poor at maintaining body temperature, they are almost permanently brooded by the adults. Reptiles and terrestrial mammals are the most frequent culprits of losses at nightjar nests. While the effective crypsis of eggs and chicks often conceals them from these predators, it also results in unintentional trampling by large mammals including people.

[*Caprimulgus manillensis*, San Salvador Island, Luzon, Philippines. Photo: Doug Wechsler/VIREO]

site until they fledge, others will move considerable distances and frequently change locations each night; for example, young White-throated Nightjars may move up to 10 m each night until about 10 days of age, and up to 20 m per night after that until they fledge. Chick movements are triggered by the adults landing nearby and calling, the offspring responding by walking, running or hopping over to them to be fed. To be given food, the chick reaches up and grabs the parent's bill; the adult then feeds

it either by regurgitating balls of insects directly into its mouth or by letting the chick take the food from inside the adult's mouth. After feeding, the chicks are then brooded at the new site.

The first set of feathers starts to appear at about 5-7 days of age. The feathers grow quickly, and in their juvenile cryptic plumage the young can be left unattended for long periods and may not be brooded during the day, although one or both parents often roost close by. If threatened, young birds adopt the flattened



According to published data, the largest clutch known for the Jungle Nightjar of eastern Asia is two eggs, although this photograph suggests that more may sometimes be found. Clutches of more than two eggs have only been reported in a few nightjar species, generally those that have received the most intensive study. It is not known whether this rare phenomenon is a result of unusually high resource levels, or egg dumping by additional females. Nightjars usually begin to incubate immediately after the first egg is laid, which leads to asynchronous hatching. This occurs after 16-19 days in the Jungle Nightjar, and the chicks tend to fledge around 17 days later.

[*Caprimulgus indicus jotaka*, central Ussuriland, Russian Far East. Photo: Yuri Shibnev/VIREO]

As this female Red-necked Nightjar takes flight from her nest, her wings almost touch over her back. During display, wing mobility is used by males of this species, and of several others, as they produce sharp clapping noises by snapping their upraised wings together. Pursuing the female in fast, direct flight, the male Red-necked claps up to fifteen times in succession. At other times, he also sings with a series of hollow "kutok" notes, a familiar sound of Iberian summer nights. While the song appears to function in both territory defence and mate attraction, wing-clapping is reserved for these courtship displays.

[*Caprimulgus ruficollis*
ruficollis,

Albacete, Spain.

Photo: Francisco Márquez]



defence posture and sit completely immobile with their eyes shut, while the adult performs a distraction display. Sometimes they remain at the site at which they were originally disturbed, but often they move to nearby cover while the adult is performing its display. Older chicks often perform a threat display if cornered, during which they stand upright, stretch out their wings, gape widely and utter a throaty hissing sound (see Voice); at times they also attempt to escape by fluttering away along the ground. Nightjar chicks often take their first flights and fledge during their third week, and become independent at about 25-35 days of age, but many also remain in family parties with their parents for many weeks.

Nest protection takes several forms, of which the first can probably be considered the actual choice of nest-site. Perhaps the most extreme example can be seen in Common Nighthawks nesting on the roofs of very tall buildings, well out of the way of most ground predators. The second and commonest method is camouflage, incubating or brooding birds sitting tightly and relying on their cryptic plumage pattern to blend in with their surroundings. When danger threatens, defence displays are performed by some parents if they are reluctant to fly away and leave their nest-sites unattended. During such displays, the adult bird usually stands upright, stretches up its neck, spreads out its wings and tail, and backs away slowly, all the time gaping widely and uttering a guttural hissing noise. Defence displays are more commonly given when there are eggs. The last lines of defence are the distraction displays, which are more usually given after hatching. The most frequent type of distraction is the broken-wing display, in which an adult feigns injury and flutters along the ground or across low vegetation, with one or both of its wings outstretched and its tail fanned. If followed, the nightjar will continue the display for a distance before flying off. Distraction displays are sometimes performed in the air, with an adult nightjar labouring or fluttering about in flight and repeatedly alighting on the ground. Some nightjars also fly to an elevated perch and perform a distraction display from there, by drooping and fluttering the wings and fanning the tail. During all forms of distraction display, nightjars are usually extremely vocal and utter various croaks, clucks or guttural hissing sounds (see Voice).

The eggs and chicks of all species are highly vulnerable to predators, especially if left unattended for long periods. Their

main enemies include snakes, lizards, diurnal raptors, owls and a vast array of carnivorous mammals. In many regions, introduced predators such as feral or domestic cats and dogs, rats (*Rattus*) and mongooses (*Herpestes*) often take a heavy toll, and island or endemic populations are particularly at risk from this threat (see Status and Conservation).

It is often maintained that nightjars try to synchronize their breeding with particular phases of the moon, so that chicks hatch and grow during periods when their parents can forage in strong moonlight, and so that young birds become independent in similar conditions. Studies have shown that some species, such as the Whip-poor-will, the Fiery-necked Nightjar, the Mozambique Nightjar and the Pennant-winged Nightjar, do often synchronize their breeding with lunar phases, while the Common Nighthawk and the Common Poorwill apparently do not. In some species, especially migratory ones such as the European Nightjar, such synchronization may occur only accidentally, as factors such as the limited time available for breeding, failed clutches, predation and weather all play their part during a particular breeding season.

In tropical or subtropical regions, rainfall can also have a dramatic effect on the breeding success of many species. In South America, species such as the little-known Scrub Nightjar sometimes attempt to rear two broods in seasons of prolonged rains but may not breed at all in dry years. In Africa, many species commence their breeding cycles towards the end of the rainy season, while in Australia two *Eurostodopus* species, the Spotted Nightjar and the White-throated Nightjar, may not breed in regions where the preceding winter has been too dry. In more temperate zones, too much rainfall can have the opposite effect and be harmful to breeding success, especially when it occurs during the breeding season itself.

Movements

As with most of their activities, the movements and migrations of nightjars usually take place at night, and as a result they remain poorly known and difficult to study. In most species, the only real indication of movement comes from the increase or decrease of numbers at a given locality, and this may be simi-



Between May and August the evocative churring song of the European Nightjar drifts over heaths, moors and woods where females lay eggs on patches of bare ground and leaves. The timing of egg-laying is apparently sometimes synchronized with lunar phases in this species, purportedly to maximize the amount of moonlight, and thus foraging efficiency, while nestlings are developing. Research shows, however, that various other factors, such as weather and the time available for breeding, combine to reduce the likelihood of this occurring. Incubation and chick-care are undertaken almost exclusively by the female, identified here by the lack of white patches in the primaries and outer rectrices. Quite often, however, she will lay a second clutch when the first brood is only 10-16 days old. If so, the male takes care of the nestlings until they reach full independence 16-22 days later, and then helps with the second brood.

[*Caprimulgus europaeus europaeus*, south-east England. Photo: Jack A. Bailey/Ardea]

larly reflected in local road-casualty figures. Given that the Caprimulgidae occur in all of the world's faunal zones, it is not surprising that a range of different migration patterns has been identified, with many species having distinctly separate breeding and non-breeding areas. Some are either wholly or partially migratory, while others undertake only local movements, some are altitudinal migrants and a few are permanently resident.

Nightjars are almost entirely insectivorous and can survive only in areas with a plentiful food supply, so any seasonal reduction in the abundance of insects will often determine a need to move to other regions. Climatic conditions are probably the most important factors affecting insect levels, and, as most nightjar species generally do not use torpor to survive seasonal "lean" periods (see Morphological Aspects), they must migrate to more suitable areas at times when there are severe food shortages.

The real long-distance migrants are to be found among the species that breed in the northern temperate zone, usually in regions that experience cold winters. These include the Canadian and North American populations of the Common Nighthawk, which winter in South America; the European Nightjar, especially in its Asian populations, which mostly move across the Arabian Peninsula and winter in south-east Africa; and the eastern Asian populations of the Jungle Nightjar, which winter mostly in South-east Asia. All of these species try to avoid long sea crossings where possible, although individuals often turn up on islands, or on ships and oil platforms at sea. There is a record from the Aleutian Islands in late May of a vagrant Jungle Nightjar from eastern Asia, but it is the Common Nighthawk that is

especially prone to vagrancy, a number of representatives of this species, mostly immatures, having been recorded in Britain and elsewhere on the eastern side of the Atlantic in autumn, with one even reaching remote Tristan da Cunha.

Many other species undertake much shorter migrations, although the distances covered are often still quite impressive. In North America, some populations of species such as the Common Poorwill and the Whip-poor-will move south to winter in the southern states and in parts of Central America, while the Chuck-will's-widow also winters in the Caribbean and in the extreme north of South America. During the autumn, northern populations of the Lesser Nighthawk and the Pauraque also vacate their breeding grounds in the USA, but their migration routes and wintering areas in Central and South America are often obscured by the presence of resident, southern populations.

Central and South American nightjars remain largely unstudied, and the migratory status of many is still almost completely unknown. Some populations of species such as the Least Nighthawk undertake reasonably long-range movements, other species move around locally, some are largely or entirely resident, and a few high-altitude species such as those that breed in the Andes generally move down into the lowlands during the non-breeding season. The most obvious migrations, however, occur in the south of the continent and involve a whole range of species, from the relatively common Band-winged and Little Nightjars to the rare Sickie-winged Nightjar. All of these migratory forms have populations that move south for the austral summer, some breeding in regions as far south as Patagonia, and return north during the winter.

In Africa, the migratory habits and routes of some nightjars are reasonably well known. A few primarily East African species, such as the Nubian and the Plain Nightjars, have partially migratory populations that breed in parts of the Arabian Peninsula and the Middle East, while several more widespread species, including the Long-tailed and Standard-winged Nightjars, are intratropical migrants that move among the savannas between the Sahara Desert to the north and the forest zone to the south. Some more southerly species, such as the Fiery-necked and Mozambique Nightjars, have rather complex migrations that are often influenced by seasonal rains, while two others, the Rufous-cheeked and Pennant-winged Nightjars, are trans-equatorial migrants that are more open to vagrancy than all other Afrotropical species.

Several Asian species within the genera *Eurostopodus* and *Caprimulgus* are known to be migratory, at least in the more northern parts of their ranges, and in Australia some populations of the Spotted Nightjar and the White-throated Nightjar have north-south migrations that appear to take small numbers into New Guinea during the non-breeding season. The nightjars that breed in New Guinea, however, are generally not migratory, and this appears to be largely true of island species and subspecies throughout South-east Asia and westwards to the Indian Subcontinent.

Altitudinal migration is perhaps the least common strategy within the Caprimulgidae, since relatively few species occur regularly in high mountainous regions or in areas far above sea-level. Of those that do, probably the majority are found in the Andes of South America, and these include the Rufous-bellied Nighthawk, the Swallow-tailed Nightjar and the Lyre-tailed Nightjar, although details of their movements, other than possible nomadic post-breeding wanderings, have yet to be studied. Data concerning the ecology of Archbold's Nightjar, the highland species of New Guinea, are rather scarce and no altitudinal movements have so far been documented. Elsewhere, other species exhibit such be-

haviour only in some parts of their ranges, an example being the Abyssinian Nightjar population breeding in Saudi Arabia, which generally occurs at altitudes of 2000-3000 m on the Raydah escarpment along the western side of the Asir Mountains but may descend to 1200-1900 m during cold winters.

Relationship with Man

Nightjars are not only crepuscular and nocturnal, they are cryptic, secretive and often silent, and are extremely difficult to study, observe or even identify in the field. In many parts of the world, they are mysterious enough to have been the subject of numerous stories and tales over the years and often feature heavily in local folklore. From one of the oldest stories has arisen the colloquial name "goatsucker", and the term is still frequently used, even to this day.

The European Nightjar is one of the most widespread and commoner species and has probably had more contact with man than just about any other nightjar. With an entirely insectivorous diet, it tends to feed in areas with a good food supply; in the past, this often meant foraging around livestock, including goats, especially in places where the animals had been corralled for the night. During the summer, it would not be uncommon for at least some of the livestock to be in breeding condition or have newly born offspring, and females would therefore often have milk dripping from their teats. The shepherds and country people, seeing the shadowy nightjars around their animals at dusk and noticing the milk early in the morning, put the two circumstances together and believed that the birds were sucking milk during the night and that, as a result, their animals would eventually be sucked dry and go blind.

This particular piece of folklore dates back at least to the time of Aristotle or even earlier, and became widespread through-

Like all members of the family, the European Nightjar is an almost exclusively aerial feeder that hunts moths, beetles and many other flying insects by sight. Its nocturnal habits leave it with few competitors apart from bats, and it has been recorded capturing up to twelve food items per minute. During the breeding season, food is delivered to nestlings and fledglings in the form of mashed up insects regurgitated in balls. When the adult visits the nest, a hungry chick reaches up to grab its bill and begs. In response, the adult inserts food into the chick's mouth or holds it up for the chick to take. The size of item brought to the nest is related to the age of chicks, with well-grown young being delivered conspicuously large helpings.

[*Caprimulgus europaeus*
europaeus,
Ringwood, Hampshire,
England.

Photo: Mike Read/
Planet Earth]





After the initial downy phase, feathers first appear on young Large-tailed Nightjars after 5-7 days. This juvenile plumage resembles that of the adult and grows very rapidly, providing the chick with camouflage that reduces the risk of predation and allows it to be left for longer periods. Indeed, the adults stop brooding the chicks after about 14 days, but often roost close by. Fledglings tend to take their first flights in the third week of life, becoming fully independent at around 35 days old. This species is common and widespread in a variety of wooded and grassy habitats between Pakistan and Australia, where it quickly colonizes deforested areas.

[*Caprimulgus macrurus bimaculatus*, Singapore.
Photo: Rolf E. Kunz]

out the whole of Europe, often earning the bird names such as goat owl or goatsucker in English, *Ziegenmelker* in German, *kozodoi* in Russian and *chotocabras* in Spanish. Indeed, the legend of the goatsucker was so widespread and well known that it also formed the basis for the scientific genus name *Caprimulgus*, *capra* being the Latin word for a nanny goat and *mulgere* meaning to milk, a "*caprimulgus*" thus being a milker of goats.

With such a huge breeding range, it is not surprising that the European Nightjar also became the subject of other myths and legends, and in Britain alone strange beliefs and local names were commonplace. In some regions, it was often associated with a mischievous spirit of the dark called Puck, from which it possibly earned the local name Puckeridge. This name, however, might also have arisen from the belief that nightjars would strike young calves with their beaks and infect them with a disease, although the skin infection concerned was most probably caused by an egg-laying fly. In other areas it was given the name Gabble Ratchet, based on the legends of the Gabriel Hounds of the wild hunt, because, when unbaptized children died, their souls were thought to disappear into nightjars. Associations with bad omens also resulted in local names such as corpse bird, corpse fowl and litch-fowl, and similar names also came into being in other countries such as Germany, where in some parts it was called *Todtenvogel* or death bird.

Superstitious beliefs about nightjars also abound in many other countries around the world, especially in remote regions, and are often based around their unseen, nocturnal habits and their strange calls. In parts of North America, the Whip-poor-will was often associated with death, while in other areas it was linked with marriage, the number of successive times it called being the number of years a man would remain a bachelor. In some regions of South America, the number of successive call notes given by a nightjar was believed to be the number of years the person who heard them would live, while, in some areas along

the Amazon, nightjars were thought to be the souls of the deceased. In parts of Australia, some Aborigines believed that the Spotted Nightjar took away babies during the night. In Sulawesi, an even stranger mythology concerns Heinrich's Nightjar, which until recently was known only from a single museum specimen taken in 1931. Also known as the Satanic or Devilish Nightjar, it was given the scientific name *Eurostopodus diabolicus* apparently as a reference to the local belief that the call of this species at night was the sound it made as it took out people's eyes.

Nightjars have never really been hunted for food, at least in any great numbers, but the eggs of some species such as the Sand-coloured Nighthawk of South America may form an important seasonal part of local diets.

Status and Conservation

Although some nightjar species are widely distributed and appear to be fairly common, the majority are so poorly known that it is difficult to gauge accurately the impact that human activities are having on their populations. Habitat destruction probably poses the greatest threat to most species, and, even allowing for the fact that a few nightjars occasionally make use of artificial or urban landscapes, they are generally intolerant of environments that have been greatly altered. After dark, nightjars like to rest in or hunt from open spaces on the ground. Unfortunately, such spaces include roads and tracks where they frequently become casualties to an ever-increasing amount of traffic, birds being run over while their vision is impaired by vehicle headlights. Many species, particularly island endemics, are also suffering as a result of predation by introduced mammals such as rats and mongooses, and the widespread reduction of insect populations through pollution and pest-control methods appears to be affecting nightjar numbers in some re-



Sadly, the European Nightjar has decreased substantially in many portions of its range.

Reduced grazing of heathlands and pastoral woodlands accelerates vegetational succession, while conversion to cultivation eliminates them altogether. These factors have reduced nightjar numbers and are compounded by catastrophic reductions in the populations of large insects, such as cockchafers (*Melolontha melolontha*), since the widespread application of pesticides on farmland.

Fortunately, modern afforestation practices provide suitable habitat for the species and although this only applies for 15-20% of the forestry cycle it has helped to maintain nightjar populations in areas from which they might otherwise have disappeared.

[*Caprimulgus europaeus europaeus*,
Surrey, England.
Photo: Frank Blackburn]

gions. Officially, six species are currently listed as globally threatened, three of which are classified as Critically Endangered, and a further eight species are considered to be Near-threatened. However, with new species and populations still being discovered, it is clear that much more information is needed in order to determine the true status of all nightjars before it becomes too late for some.

In Europe, the widespread and reasonably well-studied European Nightjar is decreasing in numbers and range in many regions. Although these declines were originally considered to be restricted to the northern and north-western limits of its breeding range, it is now clear that the species is also suffering throughout central and eastern Europe. The main reasons for the declines are generally considered to be habitat loss and pesticide use, but not all is doom and gloom, as in some countries such as Great Britain the conservation of the remaining heathland habitats and better management of woodlands and young conifer plantations has seen a small increase in numbers during the last 10-15 years. The only other European breeding species, the Red-necked Nightjar, is experiencing similar threats, and in the Mediterranean region its habitat is disappearing at an alarming rate often as a result of the ever-increasing tourist industry. The Egyptian and the Nubian Nightjars have small breeding populations just outside Europe but still within the Western Palearctic, and they, too, have declined through human pressures.

In North America, species such as the Common Nighthawk, the Common Poorwill and the Whip-poor-will are not uncommon in places, but appear to be undergoing declines at the northern limits of their breeding ranges. Of these species, the Common Nighthawk is generally the most tolerant of urban habitats and frequently occurs in towns and cities. The Lesser Nighthawk and Chuck-will's-widow are apparently faring better than most and small increases in numbers or expansions of range have been documented for some regions. The Buff-collared Nightjar is pri-

marily a Central American species with just a toehold in the extreme south-western USA; here it is officially classed as endangered, and protection measures include a complete ban on the taking of specimens for museum collections. Further to the south, this poorly known species is regarded as reasonably common in Mexico, but it is rarer in the south of its range. The Pauraque also has a small North American population in Texas, but it is primarily a Neotropical species that is generally regarded as common to fairly abundant in many parts of Central and South America.



The complexity, variability and general similarity of their plumage renders many nightjar species difficult to separate even with the benefit of prolonged views.

The combination of a white fore-wing bar, white secondary tips and a short, square tail distinguish the male Mozambique Nightjar from all other species, but these helpful features are less evident in females and immature birds.

[*Caprimulgus fossii welwitschii*,
Mvuu Camp,
Liwonde National Park,
Malawi.
Photo: Peter Steyn/Ardea]



The Long-trained Nightjar is restricted to the Atlantic forests of south-east Brazil and north-east Argentina, where it is scarce and local. During display, the male's elongated rectrices are fanned in flight, or raised while perched, to form a distinctive white "V".

The species is currently considered Near-threatened and is gradually declining as a consequence of deforestation.

To complicate conservation strategies for the species, it is an altitudinal and latitudinal migrant requiring suitable forest-edge habitat in both the breeding and non-breeding range.

[*Macropsalis forcipata*, Nova Petropolis, Rio Grande do Sul, Brazil. Photo: Haroldo Palo Jr/ NHPA]

The remaining species in Central America are, for the most part, not thought of as immediately in danger, although most are little known and infrequently seen. Several are endemic to the region, however, including two *Nyctiphrynus* poorwills and three *Caprimulgus* nightjars, and as such their populations should be closely monitored where possible. The Eared Poorwill, a Near-threatened species, and the Tawny-collared Nightjar are found only in Mexico; a disjunct population of the Ocellated Poorwill of the race *lautus* occurs in parts of Central America; the Dusky Nightjar is confined to upland forests in Costa Rica and western Panama; while the Yucatan Poorwill and the Yucatan Nightjar are, as their names suggest, largely restricted to the Yucatán Peninsula in south-eastern Mexico.

The Caribbean islands hold five endemic species which, in addition to habitat and agrochemical threats, also face the additional spectre of predation from alien omnivores and carnivores such as rats, mongooses and cats. Two of these species, the Puerto Rican Nightjar and the Jamaican Poorwill, are officially listed as Critically Endangered, and the latter is generally regarded as being the only nightjar species to have become extinct within the last 150 years. Although not positively seen since the mid-nineteenth century, all may not be lost for this always rare poorwill, since unidentified nightjars have been sighted on the island in recent years, and ornithologists need look only as far as the Puerto Rican Nightjar to see how the fortunes of these secretive birds can be dramatically different from what was previously thought. Described from a specimen taken in 1888 but not recognized as a distinct species until 1919, the Puerto Rican Nightjar was often thought of as extinct until it was rediscovered in 1961. By the early 1990's an estimated population of up to 2000 birds was thought to exist in a few dry cordillera forests in south-western Puerto Rico. Of the other endemics, the Hispaniolan Nightjar and the Near-threatened Least Poorwill are found only on Hispaniola, and the Cuban Nightjar occurs only on Cuba and the Isle of Pines. Although none of these is considered to be in immediate danger, their true status will need to be carefully monitored.

With more nightjar species than any other continent, it is not surprising that South America has more species at risk than anywhere else. Only six have so far been catalogued as being threatened or Near-threatened, but many more are poorly known and

possibly in serious trouble. The White-winged Nightjar is classified as Critically Endangered, but, although until recently it had not been seen for over 100 years, the new or potential populations lately discovered in parts of Brazil, Bolivia and Paraguay suggest that this beautiful nightjar is possibly not so rare as was previously thought. The Near-threatened species include: three endemics, namely the Choco Poorwill of western Colombia and western Ecuador, the Roraiman Nightjar, which is restricted to



Several anomalous features, such as tough, curved primaries and the apparent production of mechanical noises rather than vocalizations, suggest that the White-winged Nightjar might belong in the genus *Eleothreptus* along with the Sickie-winged Nightjar (*E. anomalus*); both species inhabit the grasslands and sparsely vegetated cerrados of South America where they are uncommon. The White-winged is only known from three widely separated sites. Adequate conservation of these legally protected areas is vital, as are further surveys in intervening regions. This species habitually perches on ant-hills or termite mounds.

[*Caprimulgus candicans*, Mbaracayú Reserve, Paraguay. Photo: K. Zyskowski/ VIREO]

After its discovery in 1888, the Puerto Rican Nightjar went unrecorded for many years and was assumed to be extinct until its rediscovery in 1961. Recent surveys have concluded that around 2000 individuals survive at a few forested sites on the coast and cordilleras of south-west Puerto Rico, including the Guánica Forest Biosphere Reserve. The species is considered Critically Endangered, mainly because of the industrial, residential and recreational development of the area, which has rapidly reduced the extent of suitable habitat. The potential negative effects of introduced mammalian predators such as cats and mongooses remain to be fully assessed.

[*Caprimulgus noctitherus*,
Guánica Forest,
Puerto Rico.
Photo: Robert Behrstock]



the Pantepui region of southern Venezuela, and the Pygmy Nightjar of north-east Brazil; and two others, the Long-trained Nightjar and the atypical Sickie-winged Nightjar. To these should be added at least two more species, the Cayenne Nightjar of French Guiana, still known only from the type specimen taken in 1917, and the newly discovered Bahian Nighthawk, described to science in 1994, about which very little is known.

In Africa only one species, Prigogine's Nightjar, is treated as globally threatened, and it is currently listed as Vulnerable. Known only from a single female taken from the Itombwe mountain forests in Zaire, the specimen lay misidentified in a Belgian museum for 35 years until it was formally recognized as a distinct species in 1990. As with the other African forest species, the Brown Nightjar and Bates's Nightjar, deforestation probably poses the greatest threat to this almost totally unknown species, but it is interesting to note that unidentified nightjars have been seen recently in the Itombwe forests and neighbouring regions, suggesting that it might not be too long before this species is rediscovered.

As if to highlight the difficulties involved in seeing, identifying and censusing nightjars, one need only turn to the case of the enigmatic Nechisar Nightjar (see Systematics). This proposed species takes its name from the national park in southern Ethiopia where it was found. Nechisar is a remote and rarely visited region that also falls within the range of another little-known east African form, the Star-spotted Nightjar, and further exploration is urgently needed to try to ascertain the current status of both forms, while hopefully also proving that the Nechisar Nightjar is a valid species.

A similar story to Prigogine's Nightjar can be seen in the Asian species, Vaurie's Nightjar, which is still known only from the type specimen taken from the deserts of Xinjiang in far western China. Although the specimen was originally obtained in 1929, its true identity remained unrecognized for 31 years, until the species was eventually described to science in 1960, although, as with the Nechisar Nightjar, its status as a distinct species is still open to doubt. Several other Asian and Oriental nightjars are rare and poorly studied, and of these only Bonaparte's Nightjar has so far been registered as Near-threatened. Several others urgently need a re-evaluation of their current status, including both

the Sumatran and the Javan populations of Salvadori's Nightjar, and the two New Guinean endemics, the Papuan Nightjar and Archbold's Nightjar. On Sulawesi there are two endemics, the Sulawesi Nightjar and Heinrich's Nightjar, both of which are poorly known and possibly at risk. The latter is especially worthy of further study as it shares a similar story to that of some other species already mentioned above: a large, dark, forest species that was described from a single female taken in 1931, it was not seen again until a possible sighting in 1993, followed by its definite rediscovery in 1996; with large-scale deforestation taking place throughout the island, urgent steps will be needed to protect its future. New Caledonia also has an endemic nightjar that has not been seen again since its original discovery in 1939. Described as the race *exul* of the White-throated Nightjar, the New Caledonian bird is nevertheless remarkably different from other forms of that species, and further studies may well prove it to be a species in its own right. Whatever it turns out to be, it is probably not common and will almost certainly require some form of immediate protection, if indeed it is eventually rediscovered in time.

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Subfamily CHORDEILINAE

Genus *LUROCALIS* Cassin, 1851

1. Semi-collared Nighthawk

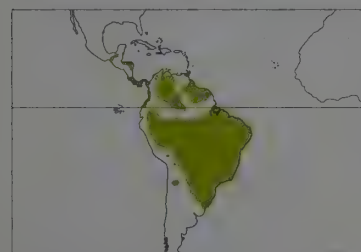
Lurocalis semitorquatus

French: Engoulevent à queue courte **Spanish:** Añapero Colicorto
German: Bändernachtschwalbe
Other common names: Short-tailed Nighthawk; Chestnut-banded/Natterer's Nighthawk (*nattereri*)

Taxonomy. *Caprimulgus semitorquatus* J. F. Gmelin, 1789, Cayenne. Formerly considered conspecific with *L. rufiventris*, with which probably forms superspecies. Race *nattereri* often considered a separate species. Population on Trinidad requires further study to ascertain subspecific status. Five subspecies currently recognized.

Subspecies and Distribution.

L. s. stonei Huber, 1923 - SE Mexico S through NE Guatemala and N Honduras to NE Nicaragua.
L. s. noctivagus Griswold, 1936 - Costa Rica and Panama S to coastal W Colombia and NW Ecuador.
L. s. semitorquatus (J. F. Gmelin, 1789) - NE Colombia and W & S Venezuela E through the Guianas, and extreme NW Brazil; also (probably this race) Trinidad and Tobago.
L. s. schaeferi Phelps & Phelps, Jr., 1952 - N Venezuela.
L. s. nattereri (Temminck, 1822) - E Ecuador, N & E Peru and Brazil S of Amazon S to N Argentina.



Descriptive notes. 19-29 cm; male 82-89 g, female 79-81 g. Sexes similar; wing-tips project well beyond tip of tail. Upperparts dark brown, speckled and spotted rufous and buff, no nuchal collar; wing-coverts dark brown, speckled and spotted rufous, tawny and buff, no scapular pattern; white throat patch; underparts dark brown, speckled greyish-white and pale buff, becoming tawny-buff barred brown on lower belly and flanks; both sexes lack white markings on wings and tail; iris dark brown, bill blackish, legs and feet brownish or greyish. Immature similar to adult, but upperparts and wing-coverts have brownish-white feathers, boldly spotted

tawny with blackish-brown tips, primaries broadly tipped brownish-white mottled brown, and all tail feathers narrowly tipped greyish-brown mottled brown. Races vary slightly in size and coloration; *nattereri* has darker, more densely barred underparts. **Voice.** Call is a repetitive, wader-like whistle, "too-it" or "to-ic", given in flight or occasionally from perches or ground; other flight calls include "kee-kee" or "kit-kit-kit" notes.

Habitat. Typically forested, wooded or partly wooded lowlands: rainforest, humid forest, forested foothills, second-growth semi-open woodland, plantations, scrubland and open countryside; also edges of forest, marshes and watercourses. Generally recorded from sea-level to 1800 m, occasionally to 2550 m.

Food and Feeding. Feeds on moths, beetles, bugs and other insects. Forages in flight.

Breeding. Breeds late Jan to early Apr in Panama, possibly May-Jun in Venezuela, Oct-Dec in Brazil, and late Nov to Jan in Argentina. Nest-site in tree alongside forest trail, near woodland clearing or beside road; no nest, egg laid in slight depression in tree branch. Clutch 1 egg, elliptical, whitish with brown and grey speckles, or light blue and streaked chestnut (possibly *nattereri* only); incubation period c. 22 days; chick covered in greyish down; fledging period c. 24 days.

Movements. Most populations possibly sedentary. Race *nattereri* may be migratory in S of range. In S Brazil, present only perhaps Oct to early Mar; possibly winters N to Venezuela.

Status and Conservation. Not globally threatened. In Central America, uncommon to frequent in Atlantic lowlands from extreme SE Mexico to Honduras; widespread and locally uncommon to common in Costa Rica; widely distributed in small numbers in Panama, where possibly increasing, resulting in slight expansion of range. In E Chiapas, Mexico, not recorded until 1989, and either previously undetected or has undergone a slight range expansion to N. In South America, widely distributed but possibly local in Trinidad; widespread and locally common in Surinam; local and uncommon in Colombia, where loss of habitat a potential threat in some regions; not recorded in Bolivia until 1980's but possibly overlooked, previous records attributable to *L. rufiventris*; common in E Paraguay but apparently much rarer in *campos cerrados* in N; in Brazil, widespread and fairly common in Amazonas drainage, common in Alagoas, and widely distributed and locally fairly common from Bahia S to Rio Grande Do Sul, where a common summer resident.

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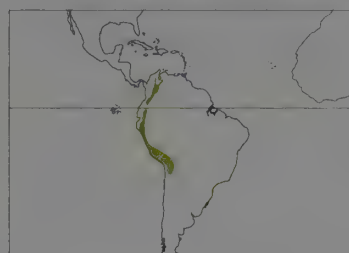
2. Rufous-bellied Nighthawk

Lurocalis rufiventris

French: Engoulevent à ventre roux **German:** Andennachtschwalbe **Spanish:** Añapero Ventrirrufo
Other common names: Taczanowski's Nighthawk

Taxonomy. *Lurocalis rufiventris* Taczanowski, 1884, Peru. Formerly considered conspecific with *L. semitorquatus*, with which probably forms superspecies. Monotypic.

Distribution. Confined to Andes, from W Venezuela to SW Colombia, S through C Ecuador, W & S Peru to W Bolivia.



Descriptive notes. 25-25.5 cm. Sexes similar; wing-tips project well beyond tip of tail. Upperparts dark brown, speckled and spotted rufous and buff, no nuchal collar; wing-coverts dark brown, speckled and spotted rufous, tawny and buff, no scapular pattern; white throat patch; underparts dark brown spotted pale tawny and greyish-white, becoming tawny-buff on belly and flanks; both sexes lack white markings on wings and tail; iris dark brown, bill blackish, legs and feet brownish. Immature similar to adult, but upperparts and wing-coverts have brownish-white feathers, boldly spotted tawny with blackish tips, primaries broadly tipped brownish-white mottled brown, and all tail feathers narrowly tipped greyish-brown mottled brown. **Voice.** Call is a series of evenly pitched or descending "kwa" notes, given in flight; also "kwo-kwo-kwo" in flight.

Habitat. Montane rainforest, cloudforest, second-growth forest and forest edge, between 1650-3000 m.

Food and Feeding. Feeds on insects. Foraging methods not documented.

Breeding. Breeding habits not documented. Breeds from late Mar in Colombia; no other data.

Movements. Sedentary and possibly partially nomadic. Specimens have been taken in Brazil, but further data not available.

Status and Conservation. Not globally threatened. Widely distributed in suitable habitat along Andes, but uncommon and local, often remaining undetected in areas with little or no ornithological coverage; recent range extension reported from Chacha in S Ecuador.

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Genus *CHORDEILES* Swainson, 1832

3. Least Nighthawk

Chordeiles pusillus

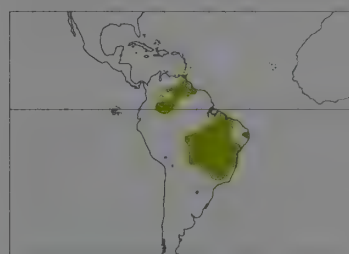
French: Engoulevent nain **German:** Gnomennachtschwalbe **Spanish:** Añapero Menudo

Taxonomy. *Chordeiles ? pusillus* Gould, 1861, Brazil.

Sympatric with *C. vielliardi* in NE Brazil. Six subspecies currently recognized.

Subspecies and Distribution.

C. p. septentrionalis (Hellmayr, 1908) - E Colombia E to W Surinam and possibly W Brazil.
C. p. esmeraldae Zimmer & Phelps, 1947 - SE Colombia, S Venezuela and extreme NW Brazil.
C. p. xerophilus Dickerman, 1988 - extreme NE Brazil (Paraíba, Pernambuco).
C. p. novaesi Dickerman, 1988 - NE Brazil (Maranhão, Piauí).
C. p. pusillus Gould, 1861 - E Brazil (Tocantins, Bahia, Goiás).
C. p. saturatus Pinto & Camargo, 1957 - WC Brazil and extreme E Bolivia.
Also (race undetermined) extreme NE Argentina.



Descriptive notes. 15-19 cm. Sexually dimorphic, though not greatly so. Upperparts generally brownish, spotted greyish-white, buff and pale tawny, no nuchal collar; wing-coverts brownish, heavily spotted buff and pale buff, faint scapular pattern; small white patch on lower throat or small white spot on either side of lower throat; underparts brown spotted and barred buffish, becoming white barred brown on belly and flanks. Male has white band across four outermost primaries, white trailing edge to inner wing and white tips to inner webs of all but central pair of tail feathers; female has thinner white wing-band and buffish trailing

edge to inner wing, and lacks white tips to some or all tail feathers. Iris dark brown, bill blackish, legs and feet brownish. Immature similar to adult. Races vary mainly in size, coloration and barring of underparts. **Voice.** Song of male is a rapid "k-k-k-k-kuree" rising in pitch and occasionally ending in long churr; flight call short "whit" or "bit".

Habitat. Usually open savanna and grassland with scattered trees and scrub, occurring in both *cerrado* and *caatinga*; also clearings along forest edges, where savanna and scrubland have become established. In Bolivia also dry, seasonally flooded grassland and rocky hillsides. Generally a lowland species, occurring from sea-level to 1000 m.

Food and Feeding. Feeds on insects. Probably catches prey in flight, though foraging methods not documented.

Breeding. Poorly known. Breeds from Jan in Colombia, possibly Oct in S Venezuela, NW Brazil and NE Argentina; two nests recently reported from E Brazil, in Bahia and Minas Gerais, in late Jan and mid-Nov respectively; no data from other localities. Nest-site on ground with stony soil and sparse bush cover; no nest, egg laid directly on ground. Clutch 1 egg, elliptical, creamy-white, faintly blotched and spotted brown and purplish-grey; chick covered in rufous-buff down.

Movements. Poorly known. Although some populations may be largely sedentary, race *esmeraldae* known to move E through N Brazil after breeding season.

Status and Conservation. Not globally threatened. Generally common to abundant in suitable habitat throughout much of range, though status in many regions poorly documented. Rather common in Guyana, especially on savannas; fairly common in NE Santa Cruz, Bolivia, more so during

Jul-Oct; seasonally common May-Sept in Mato Grosso, Brazil. Recently recorded breeding in Misiones province, NE Argentina, though race involved undetermined.
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4. Bahian Nighthawk *Chordeiles vielliardi*

French: Engoulevent du Bahia **German:** Bahianachtschwalbe **Spanish:** Añapero de Bahía
Other common names: Caatinga Nighthawk

Taxonomy. *Chordeiles vielliardi* Lencioni-Neto, 1994, Brazil. Only recently described; further study required, as species possibly more closely related to genus *Nyctiprogne* than to *Chordeiles*. Sympatric with *C. pusillus* in NE Brazil. Monotypic.
Distribution. E Brazil (N Bahia).



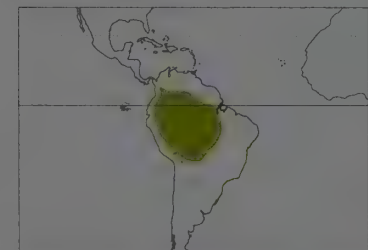
Descriptive notes. 17.5 cm. Upperparts dark chestnut spotted chestnut-brown, broadly streaked blackish-brown on crown; wing-coverts dark chestnut barred dark brown, scapulars blackish-brown edged chestnut-brown; lacks white throat patch; underparts dark chestnut-brown spotted and barred buff, becoming white barred dark chestnut on belly and flanks; lacks white markings on wings and tail; iris yellowish-brown, bill probably blackish, legs and feet yellowish-brown. Female unknown. Immature tawny than adult male, with blackish-chestnut spots on head, dark streaking on back and rump and whiter underparts; iris chestnut-brown, bill undescribed, tarsus chestnut-brown. **Voice.** Calls include series of soft "weet-weet" or "wik-wik" notes, given in flight or from perches.

Habitat. Caatinga woodland along riverbanks, especially where there are dunes and rocky outcrops.
Food and Feeding. Feeds on insects. Foraging methods not documented.
Breeding. First nest discovered in Nov 1998. No further information available.
Movements. None documented. Possibly sedentary.
Status and Conservation. Not globally threatened. Restricted-range species: present in North-east Brazilian Caatinga EBA. True status unknown, but species only recently described to science, and probably requires treatment as Data-deficient. Recorded only from two sites along R São Francisco in E Brazil; recent reports of nest and at least 30 birds in area of Januária and Mocimbinho. Research and survey work required.
Bibliography. Anon. (1995c, 1995e, 1995f, 1998c), Lencioni-Neto (1994), Stattersfield *et al.* (1998).

5. Sand-coloured Nighthawk *Chordeiles rupestris*

French: Engoulevent sable **German:** Flußnachtschwalbe **Spanish:** Añapero Blanco
Other common names: White-throated Nightjar(!)

Taxonomy. *Caprimulgus rupestris* Spix, 1825, rocky islands in the Rio Negro, Brazil. Two subspecies recognized.
Subspecies and Distribution.
C. r. xyostictus Oberholser, 1914 - C Colombia.
C. r. rupestris (Spix, 1825) - NE Ecuador, NE Peru, SE Colombia and S Venezuela E through N & C Brazil and S to C Bolivia.



Descriptive notes. 19-24 cm. Sexes similar. Upperparts pale greyish-brown, mottled and streaked brown and cinnamon, no nuchal collar; wing-coverts pale greyish-brown, cinnamon and whitish, boldly spotted with blackish star-shaped markings, no scapular pattern; white throat patch; underparts greyish-white, tinged cinnamon, barred and spotted brown, becoming buff-tinged white on belly and flanks; both sexes have large white patch across back of wings, trailing edge and wing-tips blackish-brown, and all but central pair of tail feathers white, broadly tipped brown; iris dark brown, bill blackish-grey, legs and feet greyish-brown.

Immature similar to adult but paler. Race *xyostictus* is sandier than nominate. **Voice.** Call is a trilled "rrr-wo-wo-wo", given in flight or from perches; other calls include tern-like "ow-ow-ow".
Habitat. Mainly rivers and marshes in forest and secondary growth, on rocky islands, sandy beaches and sandbars; also near riverside villages and airstrips. A lowland species, recorded from sea-level to 500 m.

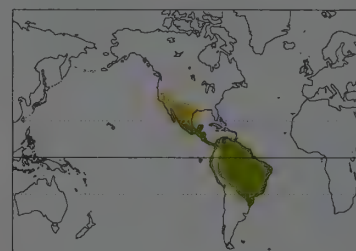
Food and Feeding. Feeds on insects, including moths and termites. Forages in flight, hunting low over sandbars and beaches or higher up above rivers. Also feeds over open country, usually near rivers, and on insects attracted to artificial lights. Often forages in loose flocks.
Breeding. Breeds during dry season in low-water periods, Jan and Jul to possibly late Sept in Colombia, May-Aug in Peru and Jun-Sept in Brazil; no data from other regions. Often in loose colonies of up to 200 pairs. Nest-site usually on sandbar or beach along river; no nest, eggs laid on sand. Clutch 1-2 eggs, elliptical, sandy-buff, possibly tinged bluish, and densely blotched and scrawled brown, laid at c. 24-hour intervals; replacement clutches may be laid if first lost through predation or flooding; incubation period c. 21 days; adults flushed from nest-site may perform injury-feigning distraction display; chick apparently not described.
Movements. Poorly known. Possibly some local movements in parts of range.
Status and Conservation. Not globally threatened. In Colombia, locally fairly common to common in suitable habitat, especially along Amazon, Orinoco and Negro rivers; very few published data from other regions. Eggs and chicks at risk from avian predators such as Bat Falcon (*Falco rufigularis*), Great Black Hawk (*Buteogallus urubitinga*), Roadside Hawk (*Buteo magnirostris*) and especially Black Caracara (*Daptrius ater*); humans probably most serious threat in many re-

gions, taking large numbers of eggs as part of local diet; reptiles such as snakes and iguanas occasionally take small numbers of eggs.
Bibliography. Allen (1995), Davis *et al.* (1994), Donahue (1994), Friedmann (1948), Groom (1989, 1992), Hilty & Brown (1986), Meyer de Schauensee & Phelps (1978), Oren & Parker (1997), Parker & Rowlett (1984), Parker *et al.* (1982), Remsen & Traylor (1989), Sargeant (1994a), Schubart *et al.* (1965), Sick (1950a, 1993, 1997), Stotz *et al.* (1996).

6. Lesser Nighthawk *Chordeiles acutipennis*

French: Engoulevent minime **German:** Texasnachtschwalbe **Spanish:** Añapero Garrapena
Other common names: Trilling Nighthawk

Taxonomy. *Caprimulgus acutipennis* Hermann, 1783, Cayenne. Birds of Baja California formerly separated in race *inferior*. Seven subspecies currently recognized.
Subspecies and Distribution.
C. a. texensis Lawrence, 1856 - SW USA S to C Mexico.
C. a. micromeris Oberholser, 1914 - N Yucatán Peninsula, Mexico.
C. a. littoralis Brodkorb, 1940 - S Mexico S through Central America to Costa Rica and possibly Panama.
C. a. acutipennis (Hermann, 1783) - Colombia E through Venezuela, Trinidad and Tobago and the Guianas and S through Brazil (absent from many parts of Amazonia) to N Bolivia and probably Paraguay.
C. a. crissalis A. H. Miller, 1959 - SW Colombia.
C. a. aequatorialis Chapman, 1923 - W Colombia, W Ecuador and possibly NW Peru.
C. a. exilis (Lesson, 1839) - W Peru and rarely extreme N Chile.



Descriptive notes. 19-23 cm; male 34-62 g, female 34-64 g. Sexually dimorphic; at rest, wing-tips reach tip of tail. Crown generally blackish-brown, rest of upperparts brownish, speckled greyish-white and boldly spotted blackish-brown; indistinct buffish or greyish-white nuchal collar; wing-coverts brownish, speckled greyish-white and greyish-brown, speckled and spotted buff, lower marginal coverts often white; scapulars blackish-brown, broadly bordered buff on outer webs; throat patch white (male) or buffish (female); underparts brownish, speckled and spotted greyish-white, cinnamon, tawny and buff, becoming buff

barred brown on belly and flanks. Male has white band across four outermost primaries and narrow white subterminal band across all but central pair of tail feathers; female has buffish or buffish-white wing-band and lacks white on tail. In flight both sexes show wing-band becoming narrower towards trailing edge of wing, with inner primaries above band spotted buffish. Iris dark brown, bill blackish, legs and feet brownish or greyish. Immature greyer or buffier than adult, with primaries and secondaries tipped greyish-white or tawny. Racial differences involve size, coloration and barring of underparts; extent of white wing and tail bands may also vary between males of some races. **Voice.** Song of male is an evenly pitched trill or slow churr. Sings in flight, from perches or ground. Courtship calls include winnowing or bleating sounds, slow, melodious trills, and long, nasal "whaa" and "whoo" calls and twangs; male also gives chucks, clucks and dove-like "c-r-rooo" calls; both sexes make guttural hissing sounds during distraction or defence displays; adult calls to offspring with soft "chunk" notes, chick utters a variety of weak "chee-uk" or "chee-ur" calls.
Habitat. Typically all types of open country, including deserts and semi-deserts, scrubland, savanna and farmland; also woodland, gardens, suburban areas, mangroves, salt lagoons and ocean beaches. Generally from sea-level to 1200 m, occasionally to 2500 m.

Food and Feeding. Diet includes crickets, beetles, winged ants, moths, mayflies, termites, dragonflies, flies, mosquitoes and bugs. Forages in flight by hunting low over savannas, fields, airstrips, roads and open country. Also feeds by making short sallies from ground. Occasionally forages during daytime, especially in overcast conditions.
Breeding. Breeds late Apr to Aug in SW USA, May-Jul/Aug in Mexico, possibly late Apr to Jul in El Salvador, Mar (perhaps) to Jul in Costa Rica, Feb-May in Trinidad and Tobago, Jun-Jul in N Colombia, Jan-Feb in S Colombia, and Feb-Mar in Ecuador; in some regions, breeding periods possibly longer than stated. Territorial; occasionally semi-colonial. Nest-site often near or beneath bush or close to vegetation, also on beach, boulders and flat roof of adobe house; no nest, eggs laid on sand, gravel, bare ground, leaf litter or possibly rock. Clutch 1-2 eggs, elliptical or elliptical-ovate, glossy, pale grey to pale creamy-white, speckled vinaceous-buff, spotted and marked grey, lilac and brown, or occasionally unmarked; incubation mainly by female, period generally 18-19 days; adults flushed from nest-site may perform distraction or defence display; eggs hatch asynchronously; chick semi-precocial, covered in buffish down with brownish mottling on upperparts; if threatened, older chicks may perform defence display by gaping and spreading wings, before running off; can fly short distances at c. 21 days of age.

Movements. Surprisingly little known; many populations possibly largely sedentary. Race *texensis* migratory, wintering from extreme S Baja California and C & S Mexico, S to Panama (Oct-Apr) and NW Colombia (Dec-Apr); occasionally also winters in S California and SW Arizona. Race *micromeris* also migratory, moving S through Central America and possibly across Gulf of Honduras; winters in Costa Rica and W Panama, possibly E to Canal Zone. S populations in South America possibly also migratory, moving N during austral winter. Often migrates in loose flocks, occasionally in large numbers. Vagrants have occurred in Ontario, Alabama, Florida, Bermuda and Trinidad.

Status and Conservation. Not globally threatened. Uncommon to locally abundant throughout range. On North American breeding grounds, locally common in California, Arizona, New Mexico and Texas; Breeding Bird Survey data for 1966-1991 suggest population generally increasing by 3.1-8.0% annually, although local declines possible in California, where loss of habitat due to mining and urbanization potential threats, and in New Mexico, where use of insecticides may be harmful. No data on territory size, though nests occasionally 25 m apart. Eggs may possibly be taken by avian predators such as Black-crowned Night Heron (*Nycticorax nycticorax*), by snakes and by mammalian predators including coyote (*Canis latrans*), kit fox (*Vulpes macrotis*), raccoon (*Procyon lotor*) and striped skunk (*Mephitis mephitis*); Loggerhead Shrikes (*Lanius ludovicianus*), Greater Roadrunners (*Geococcyx californianus*) and coyotes may possibly take chicks. Widespread and fairly common throughout much of Mexico, where also a common passage migrant and winter visitor; avian predators include Aplomado Falcon (*Falco femoralis*). Common passage migrant

through Guatemala and possibly an uncommon resident in some regions. Rare breeding species in El Salvador, first discovered nesting at two sites in Jun 1994, with 6 pairs at mouth of Río Lempa, San Vicente and 1 pair at Arcos del Espino, Usulután. Fairly common to abundant locally in Pacific lowlands of Panama, increasing between late Jul and Apr with arrival of migrants from farther N; birds once killed, dried and sold in local markets as love-charms, though no recent data on such practices. Common breeder and migrant in Trinidad, particularly common Aug-Oct. Reasonably common and locally numerous in Surinam; widespread and common in Guyana; locally uncommon to common in open, dry country in Colombia, numbers augmented outside breeding season by migrants from North & Central America. In many countries, increasing road traffic and high use of insecticides are potential threats, though no data available on effects on local populations.

Bibliography. Austin (1970a), Baicich & Harrison (1997), Belton (1984), Bent (1940), Binford (1989), Caccamise (1971, 1974), Cowles & Dawson (1951), DeGraaf & Rappole (1995), Dickerman (1981, 1982, 1985, 1986), Eisenmann (1962), ffranch (1991), Fjeldså & Krabbe (1990), Friedmann (1948), Garret & Dunn (1982), González-García (1993), Grant (1982), Haverschmidt & Mees (1994), Hayes (1995), Hilty & Brown (1986), Howell & Webb (1995a), Janos & Prather (1989), Jenkinson & Mengel (1970), Johnson (1967), Kaufman (1996), Kilgore *et al.* (1976), Komar & Rodríguez (1997), Latta & Baltz (1997), de Laubenfels (1925), Marshall (1955), Meyer de Schauensee & Phelps (1978), Miller (1937, 1959), Mills (1985, 1986), Monroe (1968), Nicol & Arnott (1974), Oberholser (1914), Pickwell & Smith (1938), Price *et al.* (1995), Pyle (1995), Ridgely & Gwynne (1989), van Rossem (1927, 1942, 1945b), Schaldach (1963), Schubart *et al.* (1965), Selander & Preece (1951), Short (1975), Sick (1993, 1997), Slud (1964), Small (1994), Snyder (1966), Stephens (1913), Stiles & Skutch (1989), Stotz *et al.* (1996), Taylor (1912), Tostain *et al.* (1992), Urban (1959), de Urioste (1994), Wetmore (1968a, 1968b), Woods (1924).

7. Common Nighthawk

Chordeiles minor

French: Engoulevent d'Amérique **German:** Falkennachtschwalbe **Spanish:** Añapero Yanqui
Other common names: Booming Nighthawk

Taxonomy. *Caprimulgus minor* J. R. Forster, 1771, no locality = South Carolina.

Formerly considered conspecific with *C. gundlachii*, but the two are sympatric in S Florida. Nine subspecies currently recognized.

Subspecies and Distribution.

C. m. minor (J. R. Forster, 1771) - most of C & S Canada S to N & NE USA.

C. m. hesperis Grinnell, 1905 - SW Canada and W USA.

C. m. sennetti Coues, 1888 - CS Canada and NC USA.

C. m. howelli Oberholser, 1914 - WC & SC USA.

C. m. henryi Cassin, 1855 - SW USA and CN Mexico.

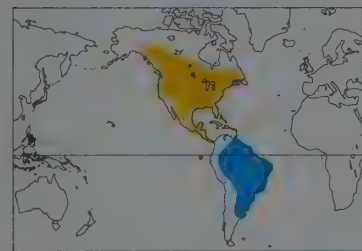
C. m. aserriensis Cherrie, 1896 - SC USA and extreme NE Mexico.

C. m. chapmani Coues, 1888 - SE USA.

C. m. neotropicalis Selander & Álvarez del Toro, 1955 - E & S Mexico, and possibly this race in Guatemala.

C. m. panamensis Eisenmann, 1962 - Nicaragua S to Panama, and possibly also N to E Honduras and Belize.

Winters in N & E South America.



Descriptive notes. 22-25 cm; male 46-107 g, female 49-101 g, average appears c. 80 g. Sexually dimorphic; at rest, wing-tips usually extend well beyond tip of tail. Crown dark brown spotted buff or tawny, upperparts brown or blackish-brown, spotted and speckled greyish-white, buff and cinnamon; no nuchal collar, although nape is spotted buff, occasionally heavily so; lesser coverts dark brown, lightly spotted greyish-white, cinnamon or pale buff, rest of wing-coverts brown, speckled and spotted greyish-white, white or pale buff, lower marginal coverts white, faint scapular pattern; supercilium greyish-white; throat patch white

(male) or buffish (female); underparts brown barred greyish-white, becoming greyish-white tinged buff and barred brown on belly and flanks, female having buffier underparts. Male has broad white band across five outermost primaries and broad white subterminal band across all but central pair of tail feathers; female has thinner, less distinct white wing-bands and lacks white on tail. In flight both sexes have white wing-band broader towards rear, inner primaries above band appearing blackish and unmarked. Iris dark brown, bill blackish, legs and feet brownish. Immature similar to adult but with underparts more heavily barred, throat patch paler and spotted, no white subterminal band on tail, and all primaries and secondaries narrowly tipped white. Races vary mainly in size, coloration, barring of underparts and, especially in males, extent of white wing and tail markings. **VOICE.** Territorial/courtship call of male is a nasal "peent", usually in flight; other calls of male include "kit-kit" or "yap-yap" in flight and "cho-ic" or "che-wip" alarms; when pairs together, male gives nasal growls or croaks, female responds with guttural "kra-a" calls; at nest, female utters variety of guttural hisses, grunts and chuckles; guttural hissing sounds given during threat or defence displays; adult uses soft, nasal "kurr" or "chuk" notes to summon offspring, chick gives soft "peep" calls.

Habitat. Favours open or semi-open arid country: savanna and open grassland, plains, grassland with scattered trees, fields, pastures, marshland, airstrips, golf courses, barren hillsides and gravelly ridges; also open forest and wood, thick spruce forest, woodland edge, burnt habitats, rocky brushland, sand dunes, beaches, desert scrub flats, coral flats with scattered vegetation, towns and cities, and edges of roads and railway tracks. In Central America, also in more humid regions. Occurs from sea-level to 2600 m.

Food and Feeding. Diet includes moths, bugs, wasps, flies, mosquitoes, mayflies, caddisflies, gnats, flying ants, plant lice, grasshoppers, locusts, crickets and beetles. Wood, vegetation and gravel are also ingested, possibly accidentally with prey. Forages in flight, occasionally very high up, over open country or water. Large numbers may forage together, feeding flocks of up to 300 having been recorded. Also feeds on insects attracted to fires and artificial lights.

Breeding. Breeds May-Jul in Canada, late Apr to Aug in N USA, late Mar to Aug in S USA, and mid-May to Aug in Central America. Occasionally double-brooded. Territorial, though occasionally breeds in loose flocks, and occasionally in loose colonies with sympatric *C. gundlachii*. Nest-site in open, barren country, in forest or wood, on beach or coral flats, in field, vineyard or garden, on stump or fence rail up to 2.5 m above ground, between rails on railway track, or on gravel roof up to 14.5 m above ground in towns and cities; no nest, eggs laid on ground, leaf litter or pine needles, gravel, brick rubble, burnt land, sand, rock or occasionally coarse moss, lichens or other vegetation.

Male performs aerial courtship display by diving steeply and producing booming sound with wings. Clutch 1-3 (usually 2, very rarely 3) eggs, elliptical and variable in colour, from dull white, greyish-white or pale creamy-white to creamy olive-buff or olive-grey, speckled and streaked grey, black, brown, olive and lilac; incubation usually by female, period generally 17-20 days; adults threatened at nest-site may perform defence or distraction displays; chick semi-precocial, covered in grey and buff down, blotched blackish-brown, fed by regurgitation, may perform threat/defence display if threatened; young often brooded for up to 20 days, though can make short flights at c. 18 days of age and catch own food at c. 25 days.

Movements. Highly migratory, breeding throughout North & Central America and wintering in South America, possibly as far S as N Patagonia. Migrates in loose flocks, large numbers often passing along favoured routes. Nominate race leaves breeding grounds late Jul to early Oct (mainly mid-Aug to early Sept), generally moving S through Central America, although some E populations may use transoceanic routes, as regular and occasionally very common autumn migrant on Bermuda. Winters in South America E of Andes, as far S as N Argentina. In spring, returning birds arrive on breeding grounds late Apr to late May (mainly middle to late May). After breeding season, race *sennetti* moves S through Colorado, Texas and Oklahoma, then possibly through E side of Central America. Race *hesperis* moves S through SW USA and Central America, although occasionally recorded E of normal routes. Race *henryi* moves SE through Central America, and possibly across Gulf of Mexico. Race *howelli* moves S through CS USA, Mexico and Nicaragua. Race *chapmani* possibly moves SE and winters from C Brazil to N Argentina. Race *neotropicalis* leaves breeding grounds in Aug and probably Sept. In spring, returning birds may begin arriving in Jan, though most not until Mar-May. Race *aserriensis* moves SE through Central America. Movements of race *panamensis* poorly documented. Vagrants have occurred in autumn in Iceland, Faeroes, Britain (mid-Sept to late Oct), at sea near Azores, and on Tristan da Cunha (late Nov).

Status and Conservation. Not globally threatened. Widespread and generally common throughout much of breeding range; widespread and locally fairly common in Mexico, where also a common passage migrant; common passage migrant in Guatemala, where may also possibly breed in small numbers; locally common to abundant in much of S Central America, e.g. in Panama a common passage migrant during spring and autumn but less common and more local as a breeding species. Widespread on South American wintering grounds, mainly E of Andes, with main range possibly E Ecuador E to S Brazil and S to Argentina. In Colombia an uncommon to fairly common autumn migrant, late Aug to late Nov, and some may overwinter; rarer in spring, Mar-Apr; winter visitor to E Ecuador, but more numerous as a passage migrant; regular winter visitor in E Peru; in Venezuela a passage migrant and possibly winters in small numbers; in Brazil a winter visitor Oct-Mar, and although most records are from S states, possibly under-recorded elsewhere; widespread and fairly common winter visitor in Paraguay; regular winter visitor in Uruguay; possibly fairly widespread in Argentina, winter range extending S to Catamarca and Buenos Aires. On breeding grounds, territory size 4-14-33-6 ha, where potential predators likely to include crows (*Corvus* sp.), falcons, especially Peregrine (*Falco peregrinus*) and American Kestrel (*Falco sparverius*), gulls (*Larus* sp.), owls (Strigidae), coyotes (*Canis latrans*), foxes (Canidae), skunks (Mustelidae), snakes, and in urban environments domestic dogs and cats; no data from wintering range. In North America, Breeding Bird Survey data show probable decline in populations, 1966-1991, in both USA and Canada, although local increases apparent over same period in Iowa, Kansas, N Dakota, Oklahoma, Utah and Vermont; listed as a species of concern (Blue List) by British Columbia Ministry of Environment 1975-1981, but not 1978, and again in 1986.

Bibliography. Abbot (1914), Aldridge & Brigham (1991), Armstrong, J.T. (1965), Armstrong, R.H. (1983), Baicich & Harrison (1997), Belton (1984), Bent (1940), Betts (1994), Binford (1989), Björklund & Björklund (1993), Blem (1972), Bowles (1921), Boyce (1980), Brigham (1988, 1989, 1990, 1994), Brigham & Barclay (1995), Brigham & Fenton (1991), Brigham, Fenton & Aldridge (1998), Brigham, Morgan & James (1995), Caccamise (1971, 1974), Campbell *et al.* (1990), Canevari *et al.* (1991), Canfield (1902), Charlton (1993), Contreras *et al.* (1990), Cyr (1995f), DeGraaf & Rappole (1995), Dexter (1952d, 1956a, 1961a, 1977), Dickerman (1990), Ehrlich *et al.* (1992), Eisenmann (1962, 1963), Ewins (1993), Firman *et al.* (1993), Fjeldså & Krabbe (1990), Fowle (1946), Garret & Dunn (1982), Goossen (1986), Gramza (1967), Hartman (1914), Hiam & Sutherland (1979), Hilty & Brown (1986), Howell, S.N.G. & Webb (1995a), Howell, T.R. (1959), Johnsgard (1979), Kaufman (1996), Laerm & Haney (1984), Larson (1970), Lasiewski & Dawson (1964), Laybourne & Post (1993), May & Short (1970), McGowan & Woolfenden (1986), Meyer de Schauensee & Phelps (1978), Miller (1925, 1937), Monroe (1968), Nicol & Arnott (1974), Oberholser (1914), Parks (1946), Patton (1924), de la Peña (1994), Poulin, Bradshaw & Graham (1996), Poulin, Grindal & Brigham (1996), Price *et al.* (1995), Raffaele *et al.* (1998), Ridgely & Gwynne (1989), Root (1988), Rust (1911, 1947), Ryan (1989), Saunders (1917), Schaldach (1963), Selander (1954), Selander & Álvarez del Toro (1955), Sellick (1916), Shields & Bildstein (1979), Sick (1993, 1997), Slud (1964), Small (1994), Stevenson *et al.* (1983), Stiles & Skutch (1989), Stotz *et al.* (1996), Sutherland (1963), Sutton & Spencer (1949), Tampion (1987), Taylor (1996), Todd *et al.* (1998), Tomkins (1942), de Vore (1996), Walbeck (1989), Wedgwood (1973, 1991, 1992), Weller (1958), Wetmore (1968a).

8. Antillean Nighthawk

Chordeiles gundlachii

French: Engoulevent pyramide **German:** Antillennachtschwalbe **Spanish:** Añapero Querequeté

Taxonomy. *Chordeiles gundlachii* Lawrence, 1856, Cuba.

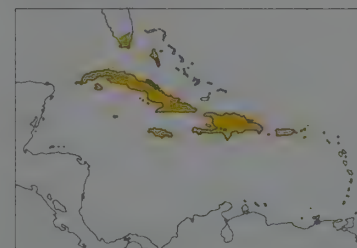
Formerly considered conspecific with *C. minor*, but the two are sympatric in S Florida. Two subspecies recognized.

Subspecies and Distribution.

C. g. vicinus Riley, 1903 - S Florida and Bahamas.

C. g. gundlachii Lawrence, 1856 - Cuba and I of Pines; Cayman Is, Jamaica, Hispaniola, Puerto Rico and Virgin Is.

Wintering grounds unknown.



Descriptive notes. 20-21 cm. Sexually dimorphic; two colour morphs, greyish and tawny; at rest, wing-tips occasionally do not reach tip of tail. Crown darkish brown spotted pale buff, upperparts brown or blackish-brown, densely spotted greyish-white, buff and cinnamon; no nuchal collar, nape being brown spotted pale buff and greyish-white; lesser coverts dark brown, lightly spotted greyish-white, pale buff or cinnamon, rest of wing-coverts brown, speckled and spotted greyish-white and cinnamon, lower marginal coverts white, faint scapular pattern; supercilium greyish-white; throat patch white (male) or buffish (female); underparts brown barred greyish-white, becoming buffish barred brown on belly and flanks. Male has

broad white band across five outermost primaries and broad white subterminal band across all but central pair of tail feathers; female has less distinct white wing-bands and lacks white on tail; in both sexes inner primaries above white wing-band appear blackish and unmarked. Iris dark brown, bill blackish, legs and feet brownish. Immature similar to adult but with underparts more heavily barred, throat patch paler and spotted, no white subterminal band on tail, and all primaries and secondaries narrowly tipped white. Race *vicinus* apparently smaller than nominate form, and has only greyish colour morph. Voice. Territorial/courtship call of male is a repetitive "chitty-chit" or "killikadik", usually given in flight; also gives nasal "penk-dik".

Habitat. Mainly open or semi-open arid country, including recently cleared areas. In Puerto Rico, also limestone forest.

Food and Feeding. Feeds on moths, beetles and other insects. Forages in flight, hunting high up over forests, shorelines, fields, pastures and towns. Feeding birds hunt alone, in pairs or in small flocks. Recorded foraging during daytime, in overcast conditions.

Breeding. Breeds mid-Apr to mid-Aug in Florida, and Apr-Aug in Bahamas, Cuba, I of Pines, Jamaica, Hispaniola and Puerto Rico. Territorial, though occasionally nests in loose colonies with sympatric *C. minor*. Nest-site in open patch of ground, among pebbles or small stones, in cavity of rough coral rock or occasionally on dirt track; no nest, eggs laid on ground, on gravel or sand. Male performs aerial courtship display flights, diving steeply and producing booming sounds with wings. Clutch 1-2 eggs, pale greyish to greenish-white, blotched and scrawled dark grey and plumbeous; incubation mainly by female, period c. 19 days; chick semi-precocial, covered in cinnamon-brown, greyish-brown or creamy-buff down with greyish-black markings.

Movements. Highly migratory, though wintering areas undocumented. Both races leave breeding grounds by Aug (probably) and Sept, and begin returning in Apr. Outside North American breeding range, recently reported from Texas and North and South Carolina.

Status and Conservation. Not globally threatened. Generally quite common throughout much of breeding range. In Cuba, extremely common Mar-Aug in open savannas and cane-fields; on Isle of Pines common on savannas and along infrequently used railway tracks. Common in Hispaniola and Puerto Rico during Aug. Race *vicinus* has apparently undergone slight range expansion: first noted on Florida Keys 1941 and now breeding there in small numbers; since 1957 also occasionally reported from Florida mainland.

Bibliography. Anon. (1998a), Baicich & Harrison (1997), Balát & González (1982), Barbour (1943), Biaggi (1983), Bond (1985), Buden (1987a, 1987b), DeGraaf & Rappole (1995), Dod (1987), Eisenmann (1962), Greene (1943), Kaufman (1996), Kepler & Kepler (1973), LeGrand (1996), Monroe (1968), Nicholson (1950, 1957), Oberholser (1914), Raffaele (1989), Raffaele *et al.* (1998), Robertson (1978), Smith (1996), Stevenson *et al.* (1983), Stotz *et al.* (1996), Vaurie (1957), Wetmore & Swales (1931).

Genus *NYCTIPROGNE* Bonaparte, 1857

9. Band-tailed Nighthawk

Nyctiprogne leucopyga

French: Engoulevent leucopyge

Spanish: Añapero Colibandeado

German: Bindenschwanz-Nachtschwalbe

Taxonomy. *Caprimulgus leucopygus* Spix, 1825, wooded shores of the Amazon.

Five subspecies recognized.

Subspecies and Distribution.

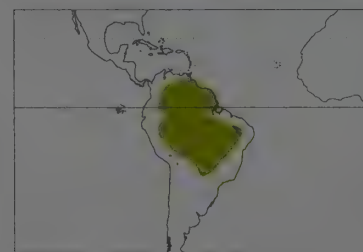
N. l. pallida Phelps & Phelps, Jr., 1952 - W & C Venezuela and possibly NE Colombia.

N. l. leucopyga (Spix, 1825) - E Venezuela E through the Guianas and N Brazil.

N. l. exigua Friedmann, 1945 - S Venezuela and E Colombia.

N. l. latifascia Friedmann, 1945 - extreme S Venezuela.

N. l. majuscula Pinto & Camargo, 1952 - W & C Brazil and N & E Bolivia; recently recorded in NE Peru.



Descriptive notes. 16-20 cm; male 23-24 g, female 23-26 g. Sexes similar. Upperparts brown, speckled pale brown, greyish-brown and cinnamon, no nuchal collar; wing-coverts brown, speckled and spotted pale brown, greyish-brown and cinnamon; scapulars blackish-brown, broadly edged buff on outer webs; small white patch on either side of lower throat; underparts brown, speckled cinnamon and barred buff, becoming greyish-white barred brown on belly and flanks. Both sexes lack white markings on wings but have prominent white band midway across three outermost tail feathers. Iris dark brown, bill

blackish, legs and feet blackish. Immature similar to adult but slightly paler and plainer. Races vary in size and intensity of overall coloration. Voice. Song of male is a treble-noted "gole-kwoik-kwak"; calls include soft, guttural "qurk" notes.

Habitat. Typically forest and savanna, usually near water: rainforest, gallery forest, forest edges, clearings, savannas and banks of large rivers; also by marshes, ponds, streams and rivers. A lowland species, recorded from sea-level to 500 m.

Food and Feeding. Diet includes beetles, bugs and ants. Forages in erratic flight, hunting over open country, marshland and riverside vegetation, along riverbanks and above water. Occasionally, feeding flocks may contain 60 or more individuals.

Breeding. Poorly known. Breeds Jan to probably Mar in Venezuela and perhaps Guyana; no data from other regions. Eggs whitish, speckled pale and dark grey.

Movements. None documented. Possibly sedentary.

Status and Conservation. Not globally threatened. Locally numerous to fairly common near water in E Colombia; fairly widespread but local in Venezuela; locally common in Amazonian Brazil and widely distributed and common, especially May-Oct, in Mato Grosso; probably fairly abundant along Rio Iténez/Guaporé in Bolivia.

Bibliography. Bates *et al.* (1989), Begazo & Valqui (1998), Davis *et al.* (1994), Dubs (1992), Friedmann (1945, 1948), Hilty & Brown (1986), Meyer de Schauensee & Phelps (1978), Oren & Parker (1997), Parker, Castillo *et al.* (1991), Parker, Parker & Plenge (1982), Remsen & Traylor (1989), Sargeant (1994a), Sick (1993, 1997), Snyder (1966), Stotz *et al.* (1996), Tostain *et al.* (1992), de Urioste (1994).

Genus *PODAGER* Wagler, 1832

10. Nacunda Nighthawk

Podager nacunda

French: Engoulevent nacunda

German: Weißbauch-Nachtschwalbe

Spanish: Añapero Ñacundá

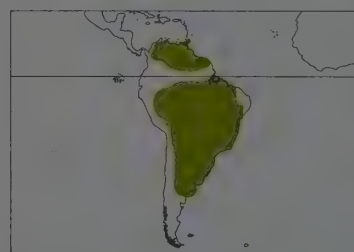
Taxonomy. *Caprimulgus nacunda* Vieillot, 1817, Paraguay.

Two subspecies currently recognized.

Subspecies and Distribution.

P. n. minor Cory, 1915 - N & C Colombia E through Venezuela, Trinidad, the Guianas and N Brazil.

P. n. nacunda (Vieillot, 1817) - E Peru E through Brazil (S of Amazon) and S to C Argentina.



Descriptive notes. 27-5-32 cm; male 142-188 g, female 124-170 g. Sexually dimorphic. Upperparts and wing-coverts brown speckled greyish-white and greyish-brown, heavily spotted blackish, no scapular pattern and no nuchal collar; large white throat patch, may show only as white band; underparts brown spotted buff, becoming white on belly and flanks, unmarked (male) or barred brown (female). Male has white band across five or six outermost primaries and broad white tips to all but central pair of tail feathers; female has smaller white wing-band and lacks white on tail. Iris brown, bill brown with dark tip, legs

and feet greyish-brown. Immature similar to adult female. Race *minor* smaller, paler and plainer than nominate. Voice. Song of male is a soft, repetitive "prrrrr-doo", usually given from ground, occasionally from perches; calls include short "whup" and melodious "cherk" notes.

Habitat. Savanna, grassland and marshland, also edges of rainforest and gallery forest, river edges, seashores and xerophytic country, from sea-level to 1000 m.

Food and Feeding. Diet includes froghoppers, beetles, bugs, winged ants, dragonflies, damselflies, Orthoptera, moths, earwigs and flies. Forages in flight, high up over marshes, reservoirs, open country and cities, and also hunts along rivers. Also feeds on insects disturbed by fires or attracted to artificial lights.

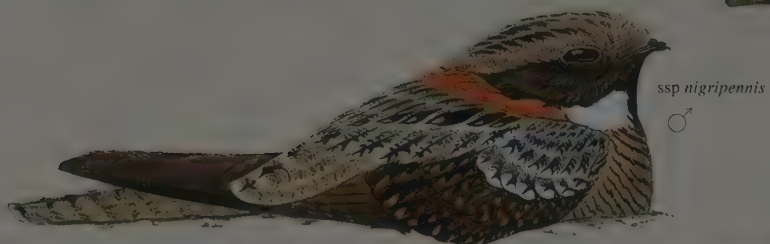
Breeding. Poorly documented. Breeds possibly Apr in Trinidad, Jan to perhaps Jun in Colombia, mid-Sept to Nov in Brazil, Nov in Uruguay and Bolivia, and Oct-Nov in Paraguay. Nest-site usually on rocky outcrop in grassland or on rocky ground beside marsh; no nest, eggs laid on leaf litter on ground. Clutch 1-2 eggs, elliptical, cream or pinkish-cream, spotted, blotched and scrawled brown, lavender and grey.

Movements. Migration patterns poorly understood. Nominat race possibly sedentary in parts of range, migratory in others, e.g. summer visitor to S Brazil (mid-Aug to mid-May) and Uruguay (Sept-Apr), casual visitor to Patagonia. Race *minor* possibly migratory; in Colombia, flocks noted Sept to late Nov in Santa Marta region, and Jul to late Oct in Meta.

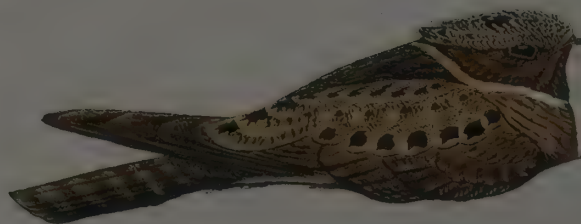
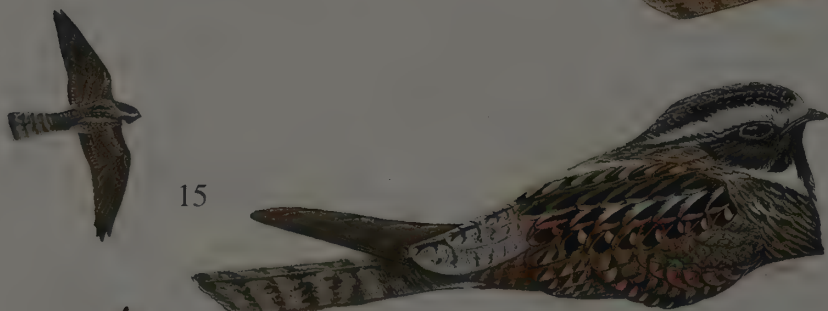
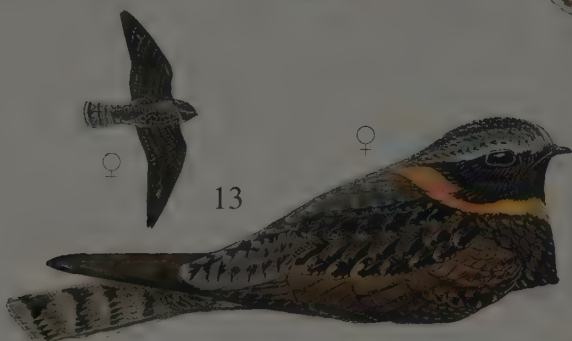
Status and Conservation. Not globally threatened. In Trinidad, locally fairly common visitor, mainly Jun-Oct, though occasional breeding suspected some years; rare in Tobago with apparently no recent records; locally common in Colombia, often forming large flocks outside breeding season; widespread but local in Venezuela, numbers in both Colombia and Venezuela also bolstered by migrants from farther S; rare in Surinam, where possibly a migrant; widespread in Guyana; in Brazil, seasonally common Apr-Oct in Mato Grosso, locally common to abundant summer visitor, mid-Aug to mid-May, in Rio Grande Do Sul; generally rather scarce to uncommon in Paraguay.

Bibliography. Belton (1984), Beltzer *et al.* (1988), Brooks *et al.* (1993), Canevari *et al.* (1991), Chubb (1910), Contreras *et al.* (1990), Davis (1993), Dubs (1992), Ifrench (1991), Friedmann (1948), Friedmann & Smith (1950), Gilliard (1941), Haverschmidt & Mees (1994), Hayes (1995), Herklots (1961), Hilty & Brown (1986), Meyer de Schauensee & Phelps (1978), Narosky & Yzurieta (1993), Parker *et al.* (1982), de la Peña (1994), Remsen & Traylor (1989), do Rosário (1996), Schubart *et al.* (1965), Short (1975), Sick (1993, 1997), Snyder (1966), Stotz *et al.* (1996), Tostain *et al.* (1992), de Urioste (1994), Wetmore (1926, 1968b).





12



Subfamily CAPRIMULGINAE

Genus *EUROSTOPODUS* Gould, 1838

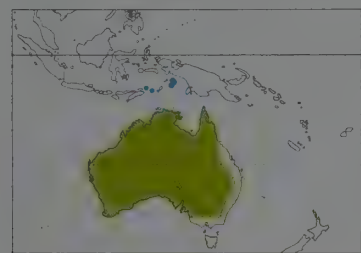
11. Spotted Nightjar

Eurostopodus argus

French: Engoulevent argus **German:** Argusnachtsschwalbe **Spanish:** Chotacabras Argos
Other common names: Spotted Eared-nightjar

Taxonomy. *Eurostopodus argus* Hartert, 1892, Australia, Aru Islands and probably New Ireland. Genus tentatively merged into *Caprimulgus* by one author, but this proposal has received very little support. Formerly listed as *E. guttatus*, but this name applies to *E. mystacalis*, of which it is a junior synonym. Birds of NW Australia formerly separated as *E. harterti*, those of Groote Eylandt as *gilberti*, and those of Banda Sea as *insulanus*, but variation appears to be limited and clinal. Monotypic.

Distribution. Most of Australia, but generally absent in coastal regions from C Queensland S to SE South Australia and Tasmania. Some birds winter N to Lesser Sunda and Aru Is.



Descriptive notes. 27–35 cm; male 81–132 g, female 75–123 g. Sexes similar. Upperparts greyish-brown speckled greyish-white; central crown broadly streaked blackish-brown edged tawny or buff; broad buffish nuchal collar; wing-coverts greyish-brown speckled greyish-white, boldly spotted buff or pale buff, prominent buffish line along scapulars; buff submoustachial stripe and large white throat patch; underparts greyish-brown spotted buff, becoming buff barred brown on belly and flanks. Both sexes have large white spot on four outermost primaries but lack white on tail. Iris dark brown, bill dark brown, legs and feet

brownish. Immature paler than adult, with smaller white spots on outer primaries; juvenile more rufous than immature. Variation clinal, birds becoming larger and darker to S. Voice. Song of male is a rapid series of ascending “whaw” notes followed by bubbling gobbles, given from ground. Alarm calls are deep barks or chirps; other calls include grunts, gurgles and pops; makes guttural hissing sounds during threat and defence displays; adult calls to offspring with low grunts, chick utters soft cheeps and trills.

Habitat. Mainly open woodland, savanna and grassland; forest and woods, mallee with eucalyptus, *Melaleuca*, *Myoporum* or *Allocasuarina*, acacia scrubland with sparse undergrowth, spinifex and tussock grassland, savanna woodland, and mangroves; prefers areas with sandy or stony ground and plenty of leaf litter. In N Australia, also low gravelly hills and ranges with rolling woodland and scrubland. On Aru Is, wintering birds frequent savanna, grassland and edges of rainforest.

Food and Feeding. Diet includes mantids, Orthoptera, bugs, lacewings, beetles, moths and winged ants. Forages in flight, often among trees and bushes, home range covering up to 1 km². Also catches prey by fluttering and hovering near vegetation and fires, or makes short sallies from ground; occasionally feeds on ground.

Breeding. Breeds Aug–Feb (possibly mainly Sept–Nov), though may not breed if preceding winter too dry. Usually single-brooded, occasionally double-brooded. Territorial, often occupying same territory for several years. Nest-site beneath tree or among stones, often near hilltop or on ridge, often close to previous year’s site; no nest, egg laid on leaf litter or bare soil. Clutch 1 egg, elliptical, glossy, and pale yellowish-green, yellowish-olive or olive-green, lightly spotted and blotched purplish-brown; probably both sexes incubate, possibly female during day with change-over at nightfall, incubation period possibly 29–33 days; adults threatened at nest-site perform defence or distraction display; chick semi-precocial, covered in reddish-brown or chestnut down, brooded by both parents, independent at c. 30 days of age.

Movements. Sedentary and locally nomadic in N, migratory and partially sedentary in S. Some S populations leave breeding grounds Mar (perhaps) to May, move N through C Australia (mainly May–Jun) and winter across N Australia from May to probably Sept. Overshooting and wintering birds also occur on islands in Banda Sea and nearby: Romang (Jul), Babar Is (Aug–Sept) and Aru Is (Apr–Sept). Return migration through C Australia Aug–Oct. N populations apparently move to well-drained, sparsely grassed hills and ridges during wet season (Nov–Mar) and return to lower-lying plains during dry season. Records from New Ireland in Bismarck Sea require further investigation. During migrations, often forms loose flocks of 10–15 birds.

Status and Conservation. Not globally threatened. Widespread but local throughout breeding range, preferring drier habitats than other Australian nightjars. Breeding territories of c. 1–2 ha and often c. 1–1.6 km apart. Few data on population levels, though 1 bird every 2 km between Normanton and Karumba, Queensland; 43 in 74 km between Roto and Mellelea, New South Wales; 9 in 13 km along Murrayville Track, Victoria; 11 in 80 km between Coolawanyah Station and Wittenoom, W Australia; local decreases by 1970’s noted in Wanjarri region of W Australia, and at Bendigo, Victoria. In Lesser Sunda, probably just a winter visitor in small numbers to Babar and Romang, though possibly under-recorded as formerly considered fairly frequent on Babar; probably also a winter visitor to Aru Is, vagrants possibly reaching New Guinea; doubtful old report from New Ireland. In Australia, potential threats include loss of suitable breeding habitat to agriculture; at night often killed by traffic on roads and tracks. Predators include feral and domestic cats, snakes and foxes. Present in several protected areas throughout range, including Wyperfeld National Park (Victoria), Round Hill Nature Reserve (New South Wales) and Two People’s Bay Nature Reserve (SW Australia).

Bibliography Barker & Vestjens (1989), Beehler *et al.* (1986), Blakers *et al.* (1984), Christidis & Boles (1994), Coates & Bishop (1997), Condon (1975), Dawson & Fisher (1969), Deignan (1950a), Higgins (1999), Johnston & Richards (1994), Lindsey (1992), Macdonald (1988), Pizzey & Doyle (1998), Rand & Gillard (1967), Robinson & Whitbourn (1961), Rose (1997a), Schodde & Mason (1981), Schodde & Tidemann (1986), Simpson & Day (1998), Strahan (1994), Tronson & Tronson (1987), White & Bruce (1986).

12. White-throated Nightjar

Eurostopodus mystacalis

French: Engoulevent moustac **German:** Bartnachtschwalbe **Spanish:** Chotacabras Bigotudo
Other common names: White-throated Eared-nightjar

Taxonomy. *Caprimulgus mystacalis* Temminck, 1826, New South Wales.

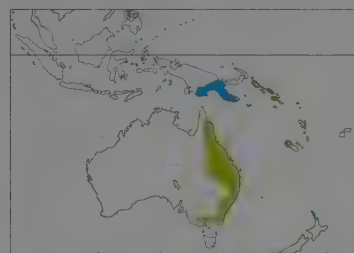
Genus tentatively merged into *Caprimulgus* by one author, but this proposal has received very little support. Formerly listed as *E. albogularis*, but name *mystacalis* has priority. Internal taxonomy worthy of further study; races *nigripennis* and *exul* may both be distinct species, with at least the former apparently differing vocally from nominate *mystacalis*. Three subspecies currently recognized.

Subspecies and Distribution.

E. m. nigripennis E. P. Ramsay, 1881 - N & C Solomon Is (including Bougainville).

E. m. exul Mayr, 1941 - New Caledonia.

E. m. mystacalis (Temminck, 1826) - E Australia, from Cape York Peninsula S through E Queensland and E New South Wales to E & CS Victoria; winters N to SC & E New Guinea.



Descriptive notes. 30–37 cm; male 98–145 g, female 140–180 g; *exul* 1 female 77 g. Sexes similar. Upperparts greyish-brown broadly streaked blackish-brown; buff or tawny-buff nuchal collar; wing-coverts greyish-brown, speckled greyish-white and spotted buff; scapulars greyish-white or greyish-brown, broadly bordered blackish-brown on outer webs; large white patch on either side of throat; underparts brown spotted rufous and greyish-white, becoming greyish-white barred brown on upper belly, rest of underparts buff or tawny-buff barred brown. Both sexes have wings regularly spotted and barred buff, white distal spot brown. Immature paler, more vinaceous, than adult. Race *nigripennis* smaller and slightly paler than nominate form, with tawnier nuchal collar and small white bands (not spots) on outer primaries, female tending to have buffish wing markings. Race *exul* extremely distinct: upperparts greyish-white streaked blackish-brown; wing-coverts greyish-brown speckled brown, broadly spotted whitish-buff; scapulars greyish-brown on inner webs, greyish-white on outer webs, broadly streaked blackish-brown in centre; similar wing markings to race *nigripennis*; no nuchal collar; breast brown, frosted greyish-white and greyish-brown. Voice. Song of male is a rapid, ascending bubbling, given from perches or in flight; female occasionally gives similar call; song of *nigripennis* described as similar to an axe hitting wood; calls include low croaks and coos, with guttural hissing sounds and barks given during distraction displays; chick gives cheeps and harsh “khaah” calls.

Habitat. In Australia, typically forest, especially eucalypt and dry sclerophyll forest, woodland, and dry, lightly forested ridges with sparse understorey; occasionally in heathland, sandy areas with thickets, or mallee scrubland. In N of range, also edges of rainforest, wet sclerophyll forest, open grassy country and borders of mangroves. In New Guinea, wintering birds frequent forest edge, savanna, scrubland, open grassland, gardens, secondary growth and marshland. On Solomon Is, usually on or near beaches and also on offshore islets. Recorded from sea-level to possibly 1650 m.

Food and Feeding. Feeds on moths, beetles, flying ants, bugs, Orthoptera and mantids. Forages in flight, usually hunting over forests, woodlands or trees, up to c. 50 m above ground. Also forages among trees and along forest edges, gulleys and streams, or makes flycatching sallies from perches or ground. Home range may be up to 100 ha or more. Often feeds on insects attracted to artificial lights.

Breeding. Breeds Sept–Feb (mainly Oct–Dec) in Australia, perhaps later in S of range, Oct–Nov on Solomon Is and possibly Aug–Sept on New Caledonia. May not breed if preceding winter extremely dry; in N Australia, some pairs may rear 2–3 young in a season when conditions ideal. Territorial, breeding territories usually 1 ha or less; nest-site usually in clearing, beneath tree, near burnt log or among rocks and stones, favourite sites on side or top of stony ridge; often breeds in same area for several years, sites within few metres of each other; no nest, egg laid on bare ground or leaf litter. Clutch 1 egg, elliptical, yellowish, buff or dark cream, spotted and blotched brown and black with underlying lavender marks, but egg of Solomons race *nigripennis* generally smaller, whitish or pinkish, and more heavily spotted; incubation usually by female during day, period generally 22–28 days; adults threatened at nest-site perform distraction display; chick semi-precocial, covered in chestnut or reddish-brown down; 1 chick made flight after 31 days.

Movements. Nominant race sedentary and partly migratory in N of range, migratory in S. On migration, often in loose flocks. In E Victoria, present Nov–Mar. S populations winter in N Australia and New Guinea. In NE Queensland, resident N of Townsville, but farther N on Atherton Tableland large numbers occasionally arrive, stay a few months and then depart. In SE New Guinea, winters (late Mar to Sept) W to Fly R and N to Astrolabe Bay. Possible vagrant reported as far N as Idenburg R in N Irian Jaya. Occurs as passage migrant through Torres Strait but recorded only Sept and possibly Oct. Race *nigripennis* on Solomon Is sedentary. Race *exul* on New Caledonia presumed sedentary.

Status and Conservation. Not globally threatened. Widespread and locally fairly common in E Australia; possibly rare to scarce winter visitor to New Guinea, though perhaps under-recorded. Race *nigripennis* probably not common on Solomon Is. Race *exul* not recorded since type specimen taken in Aug 1939 on coastal plains near Mt Panie, NW New Caledonia. On Australian breeding grounds, few data on changes in population levels, though now rare at Logan Reserve, SE Queensland, and at several sites on plains N & NW of Melbourne. Occasionally killed by road traffic at night; potential predators include snakes, foxes, dogs and feral cats. In SC New Guinea, regularly recorded at Wasur National Park.

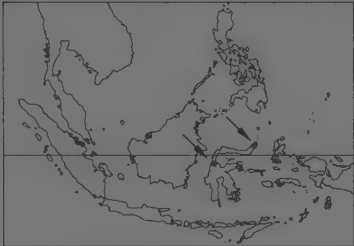
Bibliography Barker & Vestjens (1989), Beehler *et al.* (1986), Beruldsen (1980), Blakers *et al.* (1984), Christidis & Boles (1994), Coates (1985), Condon (1975), Conole (1987), Diamond (1972), Elliot (1935), Evison & Daly (1995), Hadden (1981), Hannecart & Léotard (1983), Hicks (1988c), Higgins (1999), Hollands (1991), Kutt (1994), Lindsey (1992), Macdonald (1988), Marchant (1987), Mayr (1941b, 1945), McNab & Bonaccorso (1995), Morgan (1960), O’Brien (1990), Olsen & Hayes (1994), Pizzey & Doyle (1998), Rand & Gillard (1967), Rose (1973b, 1997a), Schodde & Mason (1981), Schodde & Tidemann (1986), Simpson & Day (1998), Strahan (1994), Stronach (1981), Tronson & Tronson (1987), Wood (1995).

13. Heinrich’s Nightjar

Eurostopus diabolicus

French: Engoulevent satanique **German:** Teufelsnachtschwalbe **Spanish:** Chotacabras Diabólico
Other common names: Satanic/Devilish/Diabolical/Sulawesi(!)/Kalabat Nightjar, Heinrich’s/Satanic/Sulawesi/Celebes Eared-nightjar

Taxonomy. *Eurostopus diabolicus* Stresemann, 1931, Kumarasot, 250 m, base of Klabat Volcano, north Sulawesi.
Genus tentatively merged into *Caprimulgus* by one author, but this proposal has received very little support. Affinities of present species uncertain, but may be most closely related to other forest nightjars, *E. papuensis* and *E. archboldi*. Monotypic.
Distribution. Sulawesi.



Descriptive notes. 26 cm. Male known only from field observations. Upperparts greyish-brown, speckled and spotted brown, buff and pale tawny; crown broadly streaked blackish, no nuchal collar; wing-coverts brown, spotted and ocellated cinnamon-tawny; scapulars blackish, ocellated cinnamon on feather tips; band around throat white in male, rich buff in female; underparts brown, barred and spotted cinnamon and pale buff, becoming pale buff barred brown on belly and flanks; tail very narrowly tipped buffish. Female has small whitish spot on third and fourth outermost primaries; perhaps also present in male. Iris dark

brown, bill blackish, legs and feet dark brown. **VOICE.** Song unknown. Unidentified nocturnal calls heard in Sulawesi include a double-noted “plop-plop” and a short, bubbling trill; flight calls may include weak screams, loud “whirrip” notes and soft churrs.
Habitat. Possibly restricted to primary forest in clearings and openings, or along roads, tracks and edges. Recorded in lowland forest, hill forest and montane forest, including lightly logged areas, between 250 m and 1735 m.

Food and Feeding. Feeds on insects. Forages in flight, hunting along edges of forests and forest roads.

Breeding. No information. Possibly begins laying in Mar.
Movements. None documented. Presumably sedentary.

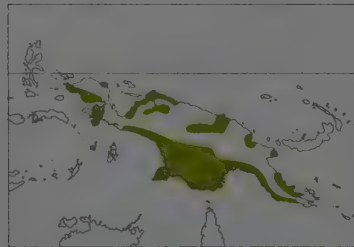
Status and Conservation. VULNERABLE. Restricted-range species: present in Sulawesi EBA. Until recently, known only from type specimen, a female, taken in Mar 1931 from Kumarasot, at base of Kalabat volcano on Minahassa peninsula in N Sulawesi; not recorded again, despite many collecting expeditions and visits by ornithologists, until Jul 1993 when a nightjar, possibly this species, was seen at c. 1700 m in Lore Lindu National Park. Rediscovered in May 1996, when birds seen in primary forest on E slopes of Gunung Nokilalaki and W slopes of Gunung Korekatimbu, close to Lore Lindu; possibly seen within the National Park on several occasions since then. Probably a rare and local species threatened by deforestation; type locality now devoid of forest and almost entirely covered by coconut plantations, at least to c. 1000 m. Some of remaining forest on Sulawesi is protected within national parks such as Lore Lindu and may conceal further populations.
Bibliography. Andrew (1992), Anon. (1998d), Bishop & Diamond (1997), Catterall (1997), Coates & Bishop (1997), Collar & Andrew (1988), Collar *et al.* (1994), Holmes & Wood (1980), King (1994), Stattersfield *et al.* (1998), Stresemann (1931b), White & Bruce (1986).

14. Papuan Nightjar

Eurostopus papuensis

French: Engoulevent papou **German:** Papuanachtschwalbe **Spanish:** Chotacabras Papú
Other common names: Papuan Eared-nightjar

Taxonomy. *Caprimulgus papuensis* Schlegel, 1866, Salawati and the opposite coast of New Guinea. Genus tentatively merged into *Caprimulgus* by one author, but this proposal has received very little support. Formerly placed in genus *Lyncornis*. Birds of E New Guinea have been separated by some authors as race *astrolabae*. Monotypic.
Distribution. Lowlands of New Guinea; also Salawati I.



Descriptive notes. 25-27.5 cm; 80-81 g (female). Sexes similar. Upperparts brown speckled and barred greyish-brown, cinnamon and rufous, broadly streaked blackish-brown on crown; no nuchal collar; wing-coverts brown speckled, spotted and tipped tawny and buff; scapulars cinnamon-buff speckled greyish-brown, boldly spotted blackish-brown; large white throat patch; underparts cinnamon-rufous barred brown, becoming buff barred brown on belly and flanks; both sexes lack white markings on wings and tail. Iris dark brown, bill blackish, legs and feet blackish. Immature similar to adult, though often

slightly paler and more heavily spotted on head. **VOICE.** Song of male is a rapid “coo-coo-coo-coo”; calls include low, guttural chattering.

Habitat. Mainly lowland rainforest in openings, clearings and glades with good ground cover of second growth, from sea-level to 400 m.

Food and Feeding. Feeds on moths and other insects. Forages in flight, hunting in forest clearings and openings or above forest canopy. Also feeds by making sallies from ground.

Breeding. Poorly known. Possibly breeds Jun-Aug. Nest-site usually among undergrowth in small clearing; no nest, egg laid on bare ground or leaf litter. Clutch 1 egg, elliptical, pinkish-brown, heavily blotched dark and pale brown, with underlying grey patches; incubation apparently by female during day.

Movements. None documented. Sedentary.
Status and Conservation. Not globally threatened. Widely distributed throughout lowlands, but generally appears to be rather scarce; not studied and no available data on population trends. Regularly recorded at Jalan Korea, near base of Cyclops Mts (Irian Jaya) and in Lakemaku Basin (Papua New Guinea).

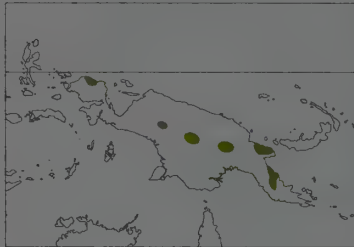
Bibliography. Andrew (1992), Bailey (1992), Beehler & Finch (1981), Beehler *et al.* (1986), Coates (1985), Hicks (1988a, 1988d, 1990), Mayr (1937b), Rand & Gilliard (1967).

15. Archbold’s Nightjar

Eurostopus archboldi

French: Engoulevent d’ Archbold **Spanish:** Chotacabras de Archbold
German: Archboldnachtschwalbe
Other common names: Archbold’s/Mountain Eared-nightjar

Taxonomy. *Lyncornis archboldi* Mayr and Rand, 1935, west slope of Mount Tafa, 2400 m, New Guinea.
Genus tentatively merged into *Caprimulgus* by one author, but this proposal has received very little support. Formerly placed in genus *Lyncornis*. Monotypic.
Distribution. Highlands of New Guinea.



Descriptive notes. 26-30 cm; 1 male 74 g, 1 unsexed c. 80 g. Sexes similar. Upperparts darkish brown spotted buff and greyish-white, crown often greyish-brown broadly streaked blackish-brown; indistinct pale greyish-brown nuchal collar; wing-coverts brown spotted cinnamon, buff and tawny; scapulars greyish-brown on upper half (not always visible) and blackish-brown distally, with cinnamon or buff spots on tips; underparts brown spotted buff or whitish, becoming buffish barred brown on belly and flanks. Both sexes have brown, unmarked wings; male has tail narrowly tipped greyish-white, female has buffish tips. Iris dark

brown, bill blackish, legs and feet brownish or dark grey. Juvenile generally white with blackish spots on upperparts. **VOICE.** Song of male is possibly a short, trilled “tchrrrt”; alarm calls of adult at nest are soft, liquid trills; when agitated, makes guttural hissing sounds.

Habitat. Montane forest with clearings and open areas of heath, at 1800-3225 m.
Food and Feeding. Diet includes moths, beetles, bugs and cicadas. Forages in flight, hunting in forest clearings and openings, or over grassy plains close to forest edges. Also forages by making short flycatching sallies from perches.

Breeding. Poorly known. Breeds Oct to early Dec throughout range. Nest-site on ground, or on bank or narrow ridge 1-1.5 m above ground; no nest, egg laid on leaf litter. Clutch 1 egg, white and unmarked; adults threatened at nest-site may perform distraction display.
Movements. None documented. Possibly sedentary.

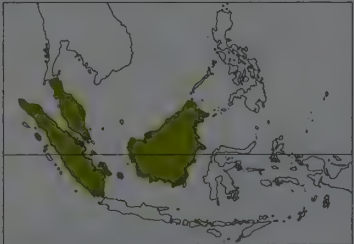
Status and Conservation. Not globally threatened. Restricted-range species: present in West Papuan Highlands EBA, Adelbert and Huon Ranges EBA and Central Papuan Mountains EBA. Widely distributed in suitable habitat at high altitudes, but generally considered rare or uncommon, though possibly under-recorded.
Bibliography. Andrew (1992), Beehler (1978), Beehler *et al.* (1986), Bishop (1987), Coates (1985), Diamond (1972), Gibbs (1996), Gregory (1995c), Hicks (1990), Mayr & Rand (1935, 1937), Rand & Gilliard (1967), Ripley (1964a), Rowland, P. (1995a), Rowland, R. (1994), Schmid (1993), Stattersfield *et al.* (1998), Tano (1996).

16. Malaysian Eared-nightjar

Eurostopus temminckii

French: Engoulevent de Temminck **Spanish:** Chotacabras de Temminck
German: Temmincknachtschwalbe
Other common names: Malaysian Nightjar, Lesser Nightjar/Eared-nightjar

Taxonomy. *Lyncornis Temminckii* Gould, 1838, Borneo.
Genus tentatively merged into *Caprimulgus* by one author, but this proposal has received very little support. Formerly placed in genus *Lyncornis*. Taxonomy requires further study. Monotypic.
Distribution. Extreme S Thailand through Peninsular Malaysia to Sumatra (including Nias, Bangka and Belitung) and Borneo.



Descriptive notes. 25-28 cm. Sexes similar. Shows distinct “ears”; upperparts brown speckled buff, pale buff and cinnamon, crown boldly spotted with blackish-brown; thin buff nuchal collar; wing-coverts brown, speckled and spotted buff, pale buff, buffish-white, tawny and cinnamon; scapulars brown speckled buff and tawny, boldly spotted blackish-brown; white throat patch or white spot on either side of lower throat; underparts buffish, indistinctly barred brown; both sexes lack white markings on wings and tail. Iris dark brown, bill horn-coloured with dark tip, legs and feet dark brown. Immature rather similar to adult but

upperparts rather cinnamon or tawny and less heavily speckled, and has less buff on underparts. **VOICE.** Call is a whistled “tut, wee-ow” given in flight; no other vocalizations have been described.

Habitat. Typically open country, open scrub forest, riparian woodland and forest edge. In Sumatra, primary and secondary forest and areas of second growth. In Borneo, dipterocarp forest, alluvial forest, scrubland, grassland, grassy swampland and coastal vegetation. Generally a lowland species, though recorded from sea-level to 1065 m.

Food and Feeding. Diet includes beetles, moths and other insects. Forages in flight, hunting over open country, rice fields and cultivated areas, forest clearings, forest edge, water and estuaries, and along rivers.

Breeding. Surprisingly little known. Possibly breeds Jan-Jul in Malay Peninsula, Mar-Apr on Belitung I, Oct-Nov in Sumatra, and from Feb in Borneo. Clutch 1-2 eggs. No further information available

Movements. None documented. Sedentary.
Status and Conservation. Not globally threatened. Local and uncommon in S Thailand; common on Malay Peninsula, where occurs in Taman Negara National Park; fairly common in Sumatra, e.g. at Gunung Leuser and Way Kambas National Parks; locally common in Borneo, where occurs in Bako and Gunung Mulu National Parks (Sarawak).

Bibliography. Andrew (1992), Bucknill & Chasen (1990), Davison (1997a), Duckworth & Kelsh (1988), Holmes & Burton (1987), Lekagul & Round (1991), Lim Kim Seng (1992), MacKinnon & Philipps (1993), Madoc (1936, 1976), van Marle & Voous (1988), Marshall (1978), Medway & Wells (1976), Nash, S.V. & Nash (1985, 1988), Riley (1938), Round (1988), Smythies (1981), Vowles & Vowles (1984), Wells (1999), Wilkinson *et al.* (1991).

17. Great Eared-nightjar

Eurostopus macrotis

French: Engoulevent oreillard **German:** Riesennachtschwalbe **Spanish:** Chotacabras Orejudo
Other common names: Greater/Philippine/Giant Eared-nightjar

Taxonomy. *Caprimulgus macrotis* Vigors, 1831, Manila.

Genus tentatively merged into *Caprimulgus* by one author, but this proposal has received very little support. Formerly placed in genus *Lyncornis*. Internal taxonomy requires further study. Five subspecies currently recognized.

Subspecies and Distribution.

E. m. bourdilloni (Hume, 1875) - SW India.

E. m. cerviniceps (Gould, 1838) - Bangladesh and NE India E to extreme S China and S through Indochina to N Malaysia.

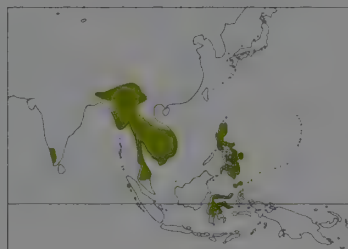
E. m. jacobsoni (Junge, 1936) - Simeulue I (off NW Sumatra).

E. m. macrotis (Vigors, 1831) - N & E Philippines (Luzon, Mindoro, Catanduanes, Marinduque, Samar, Leyte, Bohol, Dinagat, Siargao, Mindanao, Basilan).

E. m. macropterus (Bonaparte, 1850) - N & C Sulawesi, Talaud Is, Sangihe, Banggai Is and Sula Is.

Descriptive notes. 31-40 cm. Sexes similar. Shows distinct "ears"; upperparts brown speckled and spotted buff, cinnamon and greyish-white, crown boldly spotted blackish-brown; broad tawny-buff or buff nuchal collar; wing-coverts brown, speckled and spotted tawny, buff and cinnamon; scapulars brown, boldly spotted blackish-brown; large white patch, occasionally tinged buff, on either side of lower throat; underparts buffish, indistinctly barred brown; both sexes lack white markings on wings and tail. Iris dark brown, bill brownish, legs and feet flesh-brown. Races vary mainly in size and colour, although coloration in all subspecies extremely variable. **VOICE.** Call is a whistled "put, wee-oo" or "put, weew-oo", usually given in flight or from perches.

Habitat. Mainly forest: primary forest (often by rivers), secondary forest, edges and clearings, second growth, scrubland and wooded grasslands. Also more open country. Recorded generally from sea-level to 1000 m, but up to 1750 m on Sulawesi.



Food and Feeding. Diet is known to include moths, beetles, bugs and termites. Forages in flight, hunting over forest clearings, neighbouring grasslands and near habitation.

Breeding. Poorly known. Breeds Jan-May (mainly Feb-Mar) in S India and Jan-May in Malay Peninsula; in N Sulawesi, nest with egg in Oct, and species especially vocal Mar-May; fledgling immature seen in early Oct on Peleng (Banggai Is); no data from other regions. Nest-site often under thick bush or bamboo clump in lightly wooded country or bamboo jungle; no nest, egg laid on leaf litter or bare ground.

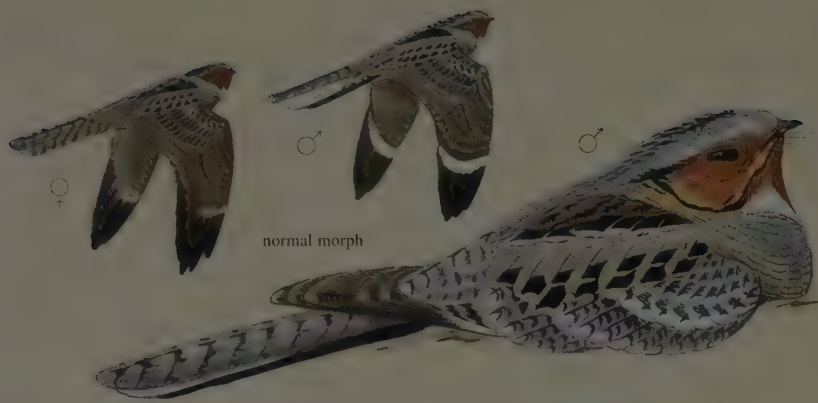
Clutch 1 egg, elliptical, creamy-white or deep

salmon-pink, marbled and blotched pale grey and reddish, especially around blunt end.

Movements. Most populations appear to be sedentary, but race *cerviniceps* local migrant to parts of NE India, arriving Aug, common until Sept, then disappears after rains.

Status and Conservation. Not globally threatened. Locally not uncommon in SW India; resident and locally migratory in NE India but rare in Bangladesh; resident in W Yunnan (S China); common in Thailand; not uncommon resident on Malay Peninsula; in past said to be locally common on Simeulue I, though no birds recorded during one-week visit in 1995; locally fairly common throughout Philippines; locally common and widespread in Sulawesi; fairly common in Banggai Is and Sula Is; possibly common throughout much of remainder of distribution. Throughout its extensive range, species occurs in several protected areas, e.g. Periyar National Park (S India), Khao Yai and Kueng Krachan National Parks (Thailand) and Nam Bai Cat Tien National Park (SC Vietnam); also Dumoga-Bone National Park (NE Sulawesi), where up to 10 birds heard and seen simultaneously over park headquarters in 1980's.

Bibliography. Ali & Ripley (1983), Cheng Tsohsin (1987), Coates & Bishop (1997), Daniels (1997), Danielsen *et al.* (1994), Deignan (1945), Delacour & Mayr (1946), Dickinson *et al.* (1991), Étiénope & Hue (1978), Gilliard (1950a), Goodman & Gonzales (1990), Grimmett *et al.* (1998), Harvey (1989), Holmes & Philipps (1996), Indrawan *et al.* (1997), Junge (1936), Lekagul & Round (1991), MacKinnon & Philipps (1993), van Marle & Voous (1988), Marshall (1978), McClure (1998), Medway & Wells (1976), Rand & Rabor (1960), Riley (1938), Ripley (1982), Round (1988), Rozendaal & Dekker (1989), Smythies (1986), Stones, Lucking *et al.* (1997), Sugathan & Natarajan (1988), Thompson *et al.* (1993), Venkatraman & Vijayan (1997), Wardill (1995), Watling (1983), Wells (1999), Whistler & Kinnear (1935), White (1977), White & Bruce (1986), Yang Lan *et al.* (1995), Zhao Zhengjie (1995).



normal morph

19

18

rufous morph



21

20



normal morph

23

normal morph

22

rufous morph

rufous morph



dark morph

25

24



rufous morph

PLATE 28

inches 4
cm 10

Genus *NYCTIDROMUS* Gould, 1838

18. Pauraque

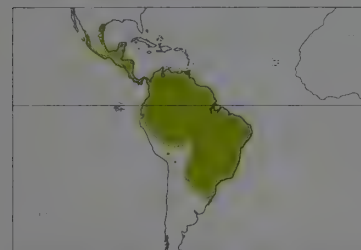
Nyctidromus albigollis

French: Engoulevent pauraqué **Spanish:** Chotacabras Pauraque
German: Pauraquenachtschwalbe
Other common names: Common Pauraque, White-necked Cuckoo

Taxonomy. *Caprimulgus albigollis* J. F. Gmelin, 1789, Cayenne. Seven subspecies recognized.

Subspecies and Distribution.

N. a. insularis Nelson, 1898 - Tres Marias Is (off W Mexico).
N. a. merrilli Sennett, 1888 - extreme S USA and NE Mexico.
N. a. yucatanensis Nelson, 1901 - W & E Mexico S to Belize and C Guatemala.
N. a. intercedens Griscom, 1929 - S Guatemala S to Costa Rica and W Panama.
N. a. gilyus Bangs, 1902 - Panama and N Colombia, perhaps to W Venezuela.
N. a. albigollis (J. F. Gmelin, 1789) - E & S Venezuela, Trinidad, the Guianas, N & NE Brazil; also (possibly this race) E & S Colombia and Ecuador S to N Bolivia.
N. a. derbyanus Gould, 1838 - C & S Brazil S to NE Argentina.



Descriptive notes. 22-28 cm; male 44-87 g, female 43-90 g. Sexually dimorphic. At rest, wing-tips reach half-way along tail. Upperparts greyish-brown tinged rufous, mottled brown and speckled greyish-white; central crown broadly streaked blackish-brown, no nuchal collar; lesser coverts chestnut to greyish, speckled brown, rest of wing-coverts greyish-brown boldly spotted buff; scapulars blackish-brown, edged and tipped buff, tawny or chestnut, especially on inner webs; buffish eye-ring and submoustachial stripe, rufous or chestnut lores and ear-coverts, and white throat patch, occasionally restricted to small white spot on either

side of lower throat; underparts greyish-brown tinged rufous, speckled and vermiculated brown, becoming buff barred brown on belly and flanks. Male has broad white band across outermost primaries, with outermost tail feather dark, next two outermost feathers largely white; female has thinner white wing-bands washed buff or tawny, and narrow white tips to second and third outermost tail feathers. Iris dark brown, bill blackish, legs and feet greyish. A less common rufous morph exists, with overall coloration tinged rufous cinnamon. Immature similar to adult, but male has thinner white wing-bands and female has tawny bands. Racial variation involves size, coloration and (in males of some subspecies) extent of white in tail. **Voice.** Song of male is a variable, whistled "wheow", "who", often preceded by soft "ko", "put" or "puk" calls, from ground or perches. Calls include rapid whips, clucks and soft whups; guttural hissing sounds, rattles and grunts are given during distraction displays; adult uses croaks and clucks when calling to offspring, chick utters soft peeps.

Habitat. Mainly forested or wooded country: forest edges and clearings, open woodland, riparian woodland, second growth and plantations. Also scrubland, open country with thickets, cultivated land, semi-arid regions, xerophytic areas, llanos, marshland and mangroves. Recorded at all altitudes from sea-level to 2300 m, occasionally to 3000 m.

Food and Feeding. Diet includes beetles, moths, butterflies, bugs, bees, wasps, antlions, ants and Orthoptera. Forages by making short sallies from ground, or by flycatching from low perches. Also hunts over open country, clearings, pastures and fields, often hawking for prey close to ground.

Breeding. Breeds Feb-Jul in Texas, late Mar to late Jun in Mexico, Feb-May in Nicaragua and Costa Rica, late Feb to Jun in Panama, Jan-May (occasionally to Aug) in Colombia, Mar-Jun in Ecuador and Venezuela, Feb-Jul in Trinidad, Mar-Oct in Surinam (though eggs found in every month except Feb), up to late Aug in French Guiana, Sept (perhaps) to Jan in SE Brazil, and Oct-Nov in Paraguay; no data from other regions but possibly Jul-Jan in S latitudes. Nest-site at base of bush or small tree, in small opening or clearing in thickets or low vegetation, in clearing or along roadside in forest, among scattered vegetation in open or semi-open country, in pasture or field, along edge of cultivated land, or among stones and boulders on dry floodplain of river or stream; no nest, eggs laid on leaf litter, bare or stony ground or pebbly sand. Clutch 1-2 eggs, elliptical, elliptical-ovate or ovate, slightly glossy, pale salmon-pink tinged ochraceous, or pinkish-buff, blotched and spotted brown, buff and lilac, markings concentrated around blunt end, or sometimes almost unmarked; incubation often by male during day, period 19-20 days; adults threatened at nest-site perform injury-feigning distraction display; chick semi-precocial, covered in brown and pinkish-buff downy.

Movements. Most populations appear to be largely sedentary. Race *merrilli* partially migratory, northern birds apparently moving S after breeding, and possibly wintering in E Mexico.

Status and Conservation. Not globally threatened. Data from many regions surprisingly scarce, but considered fairly common to abundant throughout much of range, generally occurring in a variety of habitats in tropical lowlands. Fairly common throughout much of W, E & S Mexico; abundant in many regions in Guatemala, though slightly less common in Pacific lowlands; common throughout Costa Rica; common in suitable habitat throughout Panama, though only locally so on Caribbean side and much scarcer in forests and densely wooded country. Commonest and most widespread nightjar in Colombia; very common in Venezuela; fairly common in suitable habitat in Trinidad; widespread and common throughout Guyana; common throughout Surinam; in Brazil, common in Mato Grosso, fairly common to common in Atlantic forest region, frequent in Rio de Janeiro but scarce in Rio Grande do Sul. Eggs and young may be vulnerable to trampling by domestic cattle, ground fires and, if near streams and rivers, flooding by high water. Potential predators include various species of birds, mammals and reptiles; chicks may also fall victim to fire ants.

Bibliography. Aragonés (1997b), Baicich & Harrison (1997), Barnes *et al.* (1993), Belton (1984), Bent (1940), Binford (1989), Brady (1994), Canevari *et al.* (1991), Chubb (1910), Contreras *et al.* (1990), Dearborn (1907),

Dubs (1992), French (1991), Fjeldså & Krabbe (1990), Foster & Johnson (1974), Friedmann (1948), González-García (1993), Hamilton (1948), Haverschmidt (1955b), Haverschmidt & Mees (1994), Hilty & Brown (1986), Howell, S.N.G. & Webb (1995a), Howell, T.R. (1957), Ingels (1975), Kaufman (1996), Lowery & Dalquest (1951), Meyer de Schauensee & Phelps (1978), Miller (1963), Monroe (1968), Oberholser (1925), Parker & Goerck (1997), de la Peña (1994), Price *et al.* (1995), Ridgely & Gwynne (1989), Root (1988), do Rosário (1996), Rowley (1966, 1984), Schallach (1963), Schubart *et al.* (1965), Sick (1993, 1997), Skutch (1972), Slud (1960, 1964), Snyder (1966), Stiles & Skutch (1989), Stotz *et al.* (1996), Terrill & Terrill (1986), Tostain *et al.* (1992), de Urioste (1994), West (1981), Wetmore (1968a), Zimmer (1930).

Genus *PHALAELOPTILUS* Ridgway, 1880

19. Common Poorwill

Phalaenoptilus nuttallii

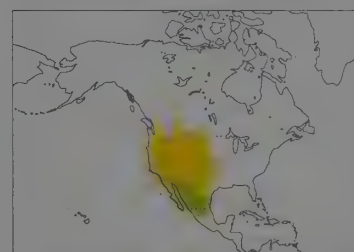
French: Engoulevent de Nuttall **German:** Winternachtschwalbe **Spanish:** Chotacabras Pachagua
Other common names: Poorwill

Taxonomy. *Caprimulgus Nuttallii* Audubon, 1844, upper Missouri between Fort Pierre and mouth of the Cheyenne River, South Dakota.

Five subspecies currently recognized.

Subspecies and Distribution.

P. n. nuttallii (Audubon, 1844) - SW Canada S through W USA to N Mexico.
P. n. californicus Ridgway, 1887 - W California and NW Baja California.
P. n. hueyi Dickey, 1928 - SE California, SW Arizona and N Baja California.
P. n. dickeyi Grinnell, 1928 - S Baja California.
P. n. adustus van Rossem, 1941 - extreme S Arizona S to C Sonora.



Descriptive notes. 18-21 cm; male 31-58 g, female 37-58 g. Sexually dimorphic, though only marginally so. Upperparts greyish-brown or greyish-white, speckled and barred brown, boldly spotted blackish-brown on crown, no nuchal collar; wing-coverts pale greyish-brown, streaked and barred blackish-brown, tipped buffish; scapulars pale greyish-buff or greyish-white with broad, almost star-shaped, blackish-brown centres; no supercilium but sides of crown often thinly edged white; blackish mask; thin, white (male) or buffish (female) submoustachial stripe; chin and throat dark brown and sides of lower throat whitish; rest

of underparts generally pale greyish-brown or buffish, barred brown. Both sexes lack white markings on wings but have all but central pair of tail feathers narrowly tipped white, more boldly so in male. Iris dark brown, bill blackish, legs and feet brownish. Immature similar to adult; juvenile dull buffish-white speckled greyish, lacking blackish-brown spotting on crown, with buffish (not white) patches on sides of lower throat and less distinct blackish-brown markings than adult, especially on underparts. Races vary slightly in size and overall coloration. **Voice.** Song of male is a melodious, whistled "poor-will-low" given from ground or perches; calls include high-pitched squeaks and, when alarmed, clucking "werk" or "quirk" sounds; guttural hissing or growling during threat and defence displays; chick utters cheeps or peeps.

Habitat. Typically arid or semi-arid country: deserts, gravelly plains, open prairie, grassy hillsides, rocky terrain with scattered vegetation or dry brush, rocky canyons and chaparral. Also open woodland, and clearings in pine or fir forest. Generally between 500 m and 1000 m, occasionally to 2500 m or higher.

Food and Feeding. Diet consists mainly of beetles, moths, cicadas, bugs, grasshoppers, locusts, flying ants and flies. Forages by making short sallies from ground or perches; also forages in flight by hawking after prey, takes insects from surfaces by fluttering close to vegetation, and occasionally takes food from ground. Also feeds on insects attracted to artificial lights.

Breeding. Probably breeds late May to Sept in N of range, Mar-Aug in S. Occasionally double-brooded, second clutch often laid within 100 m of first site. Monogamous and territorial. Nest-site usually beneath overhanging foliage or in log-strewn clearing, may be partially shaded by logs or rocks or in full sunlight; no nest, eggs laid on pine needles, bare ground, rotten log, gravel or flat rock. Clutch 2 eggs, elliptical or oval, smooth and slightly glossy, creamy-white with faint pink tinge, unmarked or faintly spotted around blunt end, laid on consecutive days; replacement clutch often laid if first lost; incubation begins with first egg, shared by both sexes, but more often by male during day, period 20-21 days; adults threatened at nest-site perform defence or distraction display; eggs hatch asynchronously, chick semi-precocial, covered in pale buff or greyish-buff down, often tinged vinaceous, fed by regurgitation; fledging at 20-23 days of age.

Movements. Well known for habit of hibernation during cold weather (see page 309). Nominate race in part sedentary and in part migratory. N populations leave breeding grounds late Sept to Nov (N birds departing earlier than S) and move S to winter throughout S parts of range from SE California and S Texas to C Mexico; S limit of wintering range poorly known. Return to breeding grounds Feb-Mar (late Apr to mid-May farther N). Race *californicus* also migratory in N of range and sedentary in S. Other races generally sedentary, although some populations of race *adustus* may undertake altitudinal movements outside breeding season. Possible vagrant recorded in Florida.

Status and Conservation. Not globally threatened. In USA, not officially listed, e.g. by US Fish and Wildlife Service, as threatened or endangered anywhere in range; in Canada, not listed by Committee on the Status of Endangered Wildlife in Canada, but red-listed by British Columbia Ministry of the Environment. In North America, uncommon in N and E of range, locally common in SW (California, Arizona, New Mexico and Colorado), local and sparsely distributed on Great Plains where slight expansion of breeding range in NE with recent records from SW North Dakota and SE Saskatchewan. Fairly common in N & C Mexico, becoming more frequent in winter after

arrival of migrants from farther N. Data from Breeding Bird Survey (1966-1991) suggest US population increasing, especially so in W of range and in Texas, but within this same period the more recent data (1982-1991) suggest possible decrease in numbers in Canada and USA; territories occasionally 0.5 km apart. Forest fires, light logging or cattle grazing may improve breeding habitats locally. Eggs and young probably taken by predators such as birds of prey, crows (*Corvus*), coyotes (*Canis latrans*), foxes (*Canidae*), badgers (*Taxidea taxus*), skunks (*Mustelidae*) and snakes. Adults may be taken by birds of prey such as Hen Harrier (*Circus cyaneus*) or Great Horned Owl (*Bubo virginianus*).

Bibliography. Aldrich (1935), Allen (1935), Austin & Bradley (1969), Baicich & Harrison (1997), Bartholomew, Howell & Cade (1957), Bartholomew, Hudson & Howell (1962), Bayne & Brigham (1995), Bent (1940), Brauner (1952, 1953), Brigham (1991, 1992), Brigham & Barclay (1992), Brigham & Trayhorn (1994), Campbell *et al.* (1990), Cink & Fiala (1972), Csada (1993), Csada & Brigham (1992a, 1992b, 1994a, 1994b), Csada *et al.* (1992), Culbertson (1946), DeGraaf & Rappole (1995), Denny (1996), Evans (1967), Fears (1975), Freemyer (1993), Glass *et al.* (1994), Goulden (1972), Horn & Marshall (1975), Howell, A.B. (1916), Howell, S.N.G. & Webb (1995a), Howell, T.R. & Bartholomew (1959), Jaeger (1948, 1949), Johnsgard (1979), Kalcounis *et al.* (1992), Kaufman (1996), Kissner & Brigham (1993), Langridge (1996), Lasiewski (1969), Lasiewski & Bartholomew (1966), Lasiewski & Seymour (1972), Lasiewski *et al.* (1971), Ligon (1970), Lowery & Dalquest (1951), Marshall (1955), McGee (1990), Meller (1954), Mengel *et al.* (1972), Miller (1950), Mills (1985, 1986), Nicol & Arnott (1974), Oberholser (1925), Orr (1948), Price *et al.* (1995), Ricciardi (1995), Root (1988), van Rossem (1941), van Rossem & Bowles (1920), Royer & Thompson (1988), Ryder (1975), Small (1994), Stebbins (1957), Stotz *et al.* (1996), Sutherland (1984), Swenson & Hendricks (1983), Swisher (1978, 1982), TenBrink (1995, 1997), Thomas *et al.* (1996), Thornburg (1953), Urban (1959), Wang & Brigham (1997), Wang *et al.* (1995), Withers (1977b), Zurowski & Brigham (1994).

Genus *SIPHONORHIS* P. L. Sclater, 1861

20. Jamaican Poorwill

Siphonorhis americana

French: Engoulevent de la Jamaïque Spanish: Chotacabras Jamaicano
German: Jamaikanachtschwalbe
Other common names: Jamaican Pauraque, Least Poorwill(!)

Taxonomy. *Caprimulgus americanus* Linnaeus, 1758, Jamaica. Formerly considered conspecific with *S. brewsteri*, and these two form a superspecies. Monotypic.
Distribution. Jamaica.



Descriptive notes. 23-25 cm. Sexually dimorphic, though only marginally so. Upperparts rufous-brown streaked blackish-brown, crown broadly streaked blackish, indistinct buffish nuchal collar; wing-coverts rufous-brown, distinctly marked blackish-brown, with small, brown-centred, pale buff spots; large white throat patch; underparts rufous-brown, boldly spotted whitish on upper belly, becoming buff barred brown towards tail. Both sexes lack white markings on wings; male has all but central pair of tail feathers narrowly tipped white, female has yellowish-buff tips. Immature plumages unknown. Voice. Unknown.

Habitat. Exact requirements unknown, but possibly dry limestone forest, semi-arid woodland or open country.

Food and Feeding. Diet probably insects. Foraging methods unknown.

Breeding. No information.

Movements. None recorded.

Status and Conservation. CRITICALLY ENDANGERED. Restricted-range species: present in Jamaica EBA. Possibly never really common and known only from four museum specimens: a male taken in or about 1844, a male taken at Savanna la Mar in Bluefields area of Westmorland in Aug 1858, a female taken at Freeman's Hall, near Albert Town in Trelawney, in Sept 1859, and a male taken near Linstead, St Thomas-in-the-Vale (Worthy Park area of St Catherine, perhaps near Spanish Town), possibly in Nov 1860. Apart from these four old museum specimens, not recorded again with certainty and often considered now extinct, although possible recent sightings have been reported from Milk R and Hellshire Hills. It has often been speculated that deforestation, and also introduction of mongooses (*Herpestes auropunctatus*) in 1872 and rats (*Rattus*), which might have preyed upon eggs and chicks, may have contributed to the disappearance of this species.

Bibliography. Anon. (1998a), Bond (1985), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Fuller (1987), Greenway (1967), Knox & Walters (1994), Raffaele *et al.* (1998), Sclater (1861), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Sutton (1981).

21. Least Poorwill

Siphonorhis brewsteri

French: Engoulevent grouillécro German: Haitinachtschwalbe Spanish: Chotacabras Torico
Other common names: Least Pauraque

Taxonomy. *Microsiphonorhis brewsteri* Chapman, 1917, Túbano, Azua, Dominican Republic. Formerly considered conspecific with *S. americana*, and these two form a superspecies. Monotypic.
Distribution. Hispaniola, including Gonáve I.

Descriptive notes. 17-21.5 cm. Sexes believed similar. Upperparts greyish-brown streaked blackish-brown, crown broadly streaked blackish, broad buff nuchal collar; wing-coverts greyish-brown, boldly spotted white; underparts dark brown, boldly spotted white on breast and becoming white, barred and vermiculated brown on belly; both sexes lack white markings on wings; male has all but central pair of tail feathers narrowly tipped white, female possibly similar or may have tips pale buff. Juvenile similar to adult, but upperparts distinctly spotted blackish-brown, and belly and flanks pale buff faintly barred brown. Voice. Song of male is a whistled "toorrrri" rising in pitch,



or a warbled "toorrrri"; calls include short, whistled "toorric" or "to-ic" and dove-like scratchy sounds.

Habitat. Typically arid or semi-arid lowlands, especially scrubby limestone woodland and areas with cactus and thorn scrub; also occurs in deciduous, coniferous or mixed forest. Recorded from sea-level to 800 m.

Food and Feeding. Diet probably consists of insects. Foraging methods not recorded.

Breeding. Poorly documented. Possibly breeds Apr-Jun. One nest-site was on top of a narrow ridge at edge of burnt land; no nest, eggs laid on ground. Eggs elliptical, dull white, spotted

pale purplish-grey, and spotted and scrawled buff and pale brown; adults threatened at nest-site may perform distraction display.

Movements. None recorded. Sedentary.

Status and Conservation. Not globally threatened. Restricted-range species: present in Hispaniola EBA. Currently considered Near-threatened. Rare, but possibly under-recorded. In late 1920's considered local in Haiti and fairly common on Gonáve I, though may have suffered from habitat loss, with large areas of scrubland often burnt off by local people, thereby restricting birds to reduced areas of native woodland; destruction of suitable habitat considered almost complete by 1970's. Apparently not reported at all between 1928 and 1969, probably owing to little or no observer coverage. In early 1970's located at 16 widespread localities in W & C Dominican Republic where previously unnoticed either because of lack of observers or as a result of a range expansion from Haiti, where habitat diminishing; several recent records from Lago Enriquillo area in centre of the island (Dominican Republic). Potential threats include predation by introduced mongooses (*Herpestes auropunctatus*) and rats (*Rattus rattus* and *R. norvegicus*) and loss of habitat through slash and burn clearance for agriculture, or taking of timber for charcoal burning.

Bibliography. Anon. (1998a), Bond (1928a, 1928b, 1985), Dod (1979, 1987, 1992), Greenway (1967), Raffaele *et al.* (1998), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Wetmore & Swales (1931).

Genus *NYCTIPHRYNUS* Bonaparte, 1857

22. Eared Poorwill

Nyctiphrynus mcleodii

French: Engoulevent aztèque German: Ohrennachtschwalbe Spanish: Chotacabras Prió

Taxonomy. *Otophanes mcleodii* Brewster, 1888, Chihuahua, Mexico. Sometimes placed in genus *Otophanes*, usually along with *N. yucatanicus*. Two subspecies recognized.

Subspecies and Distribution.

N. m. mcleodii (Brewster, 1888) - NW Mexico (Chihuahua and S Sonora to Jalisco and Colima).
N. m. rayi A. H. Miller, 1948 - CW Mexico (Guerrero).



Descriptive notes. 20-21 cm; male 31-37 g, female 24-35 g. Sexes similar. Upperparts greyish, wing-coverts spotted white, scapulars boldly spotted blackish, narrow buffish-white nuchal collar; conspicuous white band around throat; underparts greyish becoming buff lightly spotted white on belly. Both sexes lack white markings on wings, but have all but central pair of tail feathers narrowly tipped white. Iris dark brown, bill dusky or flesh with black tip, legs and feet pale pinkish-brown or greyish. A rufous morph exists, mainly in female, with general coloration rufous cinnamon to rufescent-brown. Race *rayi* darker and greyer,

with smaller white spots on wing-coverts. Voice. Song of male is a loud, abrupt "peeeyo" or "peejo"; also gives a descending, wavering "teu-uu-uu". Sings from ground or perches throughout night. Calls include short "gwik" or "wuik"; both sexes utter soft "chuk" notes; if disturbed, female may give a short, trilled churr.

Habitat. Mainly open woodland of pine and/or oak, usually in semi-arid, mountainous terrain; also woodland edge, wooded gulleys, oak-covered hillsides below cloudforest, and occasionally overgrown fields with scattered trees. Recorded from 600-2500 m.

Food and Feeding. Feeds on insects, especially beetles and moths. Forages by making short flycatching sallies from trees or ground.

Breeding. Poorly documented. Possibly breeds Apr-Jun. Nest-sites recorded in short grass at cliff base and in clumps of pines (*Pinus teocote*); no nest, eggs laid on ground or pine needles. Clutch 2 eggs, ivory-white, unmarked.

Movements. Mainly sedentary, although occasionally may undertake local movements as race *rayi* reported as a casual visitor to state of Oaxaca.

Status and Conservation. Not globally threatened. Currently considered Near-threatened. A little-known species endemic to W Mexico, where locally rare to fairly common in suitable habitat. Widely distributed in SW Jalisco and neighbouring Colima, possibly not uncommon in C Sierra Madre del Sur, Guerrero. No data available from other regions.

Bibliography. Anon. (1998a), Arnold (1971), Binford (1989), Hernández-Baños *et al.* (1995), Howell & Webb (1994, 1995a), Miller (1948), Ridgway (1912b), Schaldach (1963), Schaldach & Phillips (1961), Stotz *et al.* (1996).

23. Yucatan Poorwill

Nyctiphrynus yucatanicus

French: Engoulevent du Yucatan Spanish: Chotacabras Yucateco
German: Yucatannachtschwalbe

Taxonomy. *Caprimulgus yucatanicus* Hartert, 1892. Tizimin, Yucatán, Mexico. Sometimes placed in genus *Otophanes* along with *N. mcleodii*, or in monotypic *Nyctagreuus*. Monotypic.

Distribution. Yucatán Peninsula of Mexico, N Guatemala and N Belize.



Descriptive notes. 19.5–22 cm; 1 male 21 g. Sexes similar. Upperparts brown streaked blackish-brown, lightly spotted buffish-white on wing-coverts; narrow and indistinct buffish nuchal collar and large white throat patch; underparts brown narrowly streaked blackish-brown on breast, becoming brown or brownish-buff spotted white on belly. Both sexes lack white markings on wings, but have all but central pair of tail feathers narrowly tipped white. Iris dark brown, bill blackish, legs and feet brown. A rufous morph exists, apparently mostly in female, with overall coloration pinkish-cinnamon. Immature plumages unknown.

Voice. Song of male is a repetitive “weeo, weeo, weeo” given from perches. Other calls include liquid clucking sounds and “week, week” notes.

Habitat. Typically scrubland, deciduous forest and open woodland, usually in arid or semi-arid lowlands; also farmland and fields, second growth and thorny woodland. Recorded from sea-level to 250 m.

Food and Feeding. Probably feeds on insects. Forages by making short sallies from trees or ground.

Breeding. Poorly documented. Breeds Apr–Jun in Guatemala; no data from other regions. No nest, eggs laid on leaf litter on ground. Eggs elliptical, glossy, buffish, speckled brown; adults threatened at nest-site perform injury-feigning distraction display on ground.

Movements. None documented. Possibly sedentary.

Status and Conservation. Not globally threatened. Endemic to Yucatán Peninsula of Mexico, with range extending S into Belize and N Guatemala. During 1940’s and 1950’s considered fairly abundant in lowland deciduous forests, less frequent in areas of second growth within rainforest zone. First recorded S of San Ignacio, Belize, in Feb 1990, furthest S locality for this species. Probably remains fairly common throughout range, though few data available.

Bibliography. Anon. (1998a), Hardy & Straneck (1989), Howell & Webb (1995a), Howell *et al.* (1992), Land (1970), Paynter (1955), Pierson (1986), Ridgway (1912b), Russell (1964), Smithe (1966), Stotz *et al.* (1996), Vallely & Whitman (1997), Van Tyne (1935).

24. Ocellated Poorwill

Nyctiphrynus ocellatus

French: Engoulevent ocellé **German:** Augennachtschwalbe **Spanish:** Chotacabras Ocelado

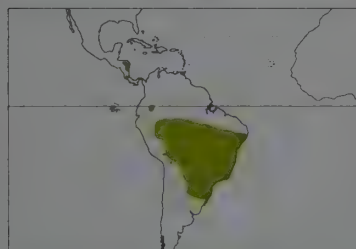
Taxonomy. *Caprimulgus ocellatus* Tschudi, 1844, Peru.

Until recently considered conspecific with *N. rosenbergi*, but differs vocally and may not even be closely related. Two subspecies currently recognized.

Subspecies and Distribution.

N. o. lautus W. deW. Miller & Griscom, 1925 - NE Nicaragua, NW Costa Rica and possibly Panama (Canal Zone); recently discovered breeding in extreme E Honduras.

N. o. ocellatus (Tschudi, 1844) - CS Colombia, NE Ecuador and E Peru to E Brazil and S through Bolivia and Paraguay to NE Argentina and extreme S Brazil.



Descriptive notes. 20–21 cm; male 35–43 g, female 29–44 g. Sexes similar. Upperparts and wing-coverts almost uniformly dark greyish-brown, no nuchal collar; scapulars and some wing-coverts boldly spotted blackish-brown, spots bordered rufous or buffish; white band around throat; underparts dark greyish-brown, spotted white on belly. Both sexes lack white markings on wings, but have all but central pair or two pairs of tail feathers narrowly tipped white. Iris dark brown, bill blackish, legs and feet dark brown. A rufous morph exists, paler and more reddish-brown overall. Immature plumages unknown. Race *lautus* smaller with

narrower white tips to outer tail feathers. **Voice.** Song of male is a repetitive trilled “preeo” given from perches or ground, mainly at dusk. Call is a soft, guttural “wah, wah, wah”.

Habitat. Prefers lowland forest with open understorey and small, shady clearings; also occurs in dense second-growth forest with plenty of small trees and vines. Reported from sea-level to 1350 m.

Food and Feeding. Feeds on moths, beetles, cockroaches (including Blattidae), katydids (including Tertrigoniidae) and fireflies (including Lampyridae). Forages by making short sallies from low perches.

Breeding. Poorly documented. Possibly breeds Mar–Apr in Costa Rica and Nicaragua, and Oct–Nov in Peru; a female incubating 2 eggs in May in Honduras; no data from other regions. Nest-site often below overhanging foliage; no nest, eggs laid on leaf litter. Clutch 2 eggs, elliptical, off-white to pinkish-white, unmarked or faintly spotted reddish.

Movements. None recorded. Sedentary.

Status and Conservation. Not globally threatened. As a forest inhabitant with nocturnal habits, difficult to find, e.g. not recorded in Bolivia until 1940’s, possibly because of under-recording rather than range expansion. Recently discovered (1997) breeding in E Honduras, at Las Marias in Río Plátano Biosphere Reserve, situated in region of over 250,000 ha of relatively undisturbed lowland rainforest, with small human population. Small breeding population in NW Caribbean lowlands of Costa Rica may be result of a range expansion from Nicaragua, where first discovered in 1909. As yet, not reliably recorded in Panama, though a sight report from Canal region, Mar 1978. Local in Colombia, probably occurring in forests on E slope of E Andes. In Peru, occurs in Manu National Park and Tambopata Reserve. Fairly common in Augusto Ruschi Biological Reserve, Atlantic forest region, Brazil; also found in Sooretama Biological Reserve, Espírito Santo. Rare in E Paraguay. Loss of habitat due to deforestation probably potential threat in some regions, especially to Central American population.

Bibliography. Allen (1995), Anderson *et al.* (1998), Butler (1979), Canevari *et al.* (1991), Chebez (1994), Donahue (1994), Gyldenstolpe (1945b), Hayes (1995), Hilty & Brown (1986), Madroño & Esquivel (1997), Madroño *et al.* (1997), Miller & Griscom (1925a), Narosky & Yzurieta (1993), Parker & Goerck (1997), Parker *et al.* (1982), de la Peña (1994), Pereyra (1950), Remsen & Traylor (1989), Ridgely & Gwynne (1989), do Rosário (1996), Schubart *et al.* (1965), Sick (1993, 1997), Stiles (1988), Stiles & Skutch (1989), Storer (1989), Stotz *et al.* (1996), Straube & Bornschein (1991, 1995).

25. Choco Poorwill

Nyctiphrynus rosenbergi

French: Engoulevent du Choco

Spanish: Chotacabras del Chocó

German: Rosenberg-Nachtschwalbe

Taxonomy. *Caprimulgus rosenbergi* Hartert, 1895, Río Dagua, Colombia.

Formerly considered conspecific with *N. ocellatus*, but differs vocally and may not even be closely related. Monotypic.

Distribution. Chocó region of W Colombia and NW Ecuador.



Descriptive notes. 19.5–21 cm; 1 female 52 g. Sexes similar. Upperparts and wing-coverts darkish brown, washed cinnamon and rather heavily spotted blackish-brown, with two or three large white spots on inner greater coverts; no nuchal collar; large white throat patch; underparts darkish brown, washed cinnamon on breast, greyish-white on belly. Both sexes lack white markings on wings but have all tail feathers narrowly tipped white. Iris dark brown, bill blackish or grey with black tip, legs and feet greyish or purplish-brown. Immature similar to adult but markings on upperparts and breast more chestnut, and lacks white spots on

inner greater coverts; little colour variation noted, although male can be rather blackish. **Voice.** Song of male is a short, resonant “kwor, kwor, kwecé”, final note being whistled. Sings mainly at dusk and dawn. Calls include “whee, whurrr” or “kwee, whurrr” notes, first note rising in pitch, second trilled and descending.

Habitat. Mainly primary forest but also adjacent secondary forest, from sea-level to 900 m.

Food and Feeding. Feeds mainly on moths and beetles (including Scarabaeidae and Curculionidae). Forages by hawking for insects above forest canopies and in clearings.

Breeding. Almost entirely unknown. Breeds Mar–Jun in Ecuador (chicks found mid-Apr) and May–Jun in Colombia (chicks found early Jun).

Movements. None recorded. Sedentary.

Status and Conservation. Not globally threatened. Restricted-range species: present in Chocó EBA. Currently considered Near-threatened. In SW Colombia, possibly locally widespread in suitable habitat W of Andes; fairly common within primary forest at Alto Tambo, NW Ecuador, where habitat remains largely intact and species possibly not under immediate threat. No data from other localities.

Bibliography. Chapman (1917), Collar *et al.* (1994), Hilty & Brown (1986), Ridgway (1912b), Robbins & Ridgely (1992), Stattersfield *et al.* (1998), Stotz *et al.* (1996).



26



ssp rufus

27



28



ssp otiosus



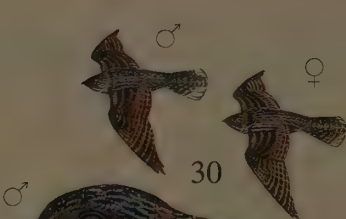
ssp minimus

LATE 29

inches 5
cm 13



29



30



31



ssp vociferus

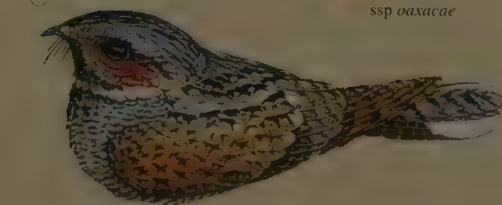
ssp oaxacae



32



33



34



35



36



ssp arizonae

Genus *CAPRIMULGUS* Linnaeus, 1758

26. Chuck-will's-widow

Caprimulgus carolinensis

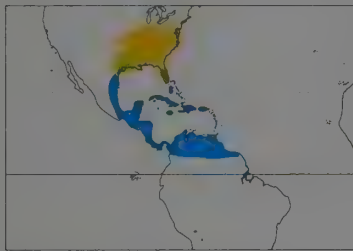
French: Engoulevent de Caroline **Spanish:** Chotacabras de la Carolina

German: Carolinanachtschwalbe

Other common names: Carolina Chuck-will

Taxonomy. *Caprimulgus carolinensis* J. F. Gmelin, 1789, South Carolina. May form superspecies with *C. rufus*, with which has even been considered conspecific, but differs notably in both voice and morphology. Monotypic.

Distribution. E North America S from Kansas, extreme S Ontario and Massachusetts. Winters from S USA (SE Texas and Louisiana) S through Central America to N South America; and from N Florida S through Bahamas to Greater Antilles, and E to Virgin Is.



Descriptive notes. 27-34 cm; male 94-137 g, female 114-118 g. Sexually dimorphic. Upperparts brown, broadly streaked blackish-brown, with narrow and indistinct tawny-buff nuchal collar; wing-coverts brown, heavily spotted buff and buffish-white; scapulars boldly spotted blackish; narrow white or buffish-white band around lower throat; underparts brown, speckled and spotted tawny and buff, becoming buff barred brown on belly; both sexes lack white markings on wings. Male has white inner webs to three outermost tail feathers, outer webs being tawny, speckled or barred blackish; female lacks white on tail. Iris dark brown, bill

dusky flesh with black tip, legs and feet dull flesh. Generally larger than *C. rufus*; larger and less variegated than *C. vociferus*. Immature similar to adult female. **Voice.** Song of male is a loud, repetitive "chuk, weeo, weeo"; song variable and may be faster, higher pitched, or more muted. Sings from perches, mainly at dusk, dawn and throughout moonlit nights, and occasionally during daytime; sings less strongly while breeding. Flight calls, given by both sexes, include clucks, growls and deep "quok" notes; guttural hissing sounds are uttered during threat/defence displays.

Habitat. Generally deciduous wood and forest, mixed woodland of pines and oaks, and wooded oak groves; also suburban habitats, open country, pastureland and coniferous forest. Outside breeding season, also in thick woodland, open woodland, scrub and palmetto thickets, tangled riverside vegetation, mature hedgerows and second-growth woodland. Reported from sea-level to 2600 m. **Food and Feeding.** Feeds on moths, flying ants, cicadas, crickets, grasshoppers, damselflies, dragonflies, beetles (including Carabidae, Cerambycidae, Elateridae and Scarabaeidae), bugs, flies and small birds (including Emberizidae, Trochilidae and Hirundinidae). Also known to take bivalves. Hunts in flight along woodland edges and over open areas, often flying low over ground, and also forages by making short flycatching sallies from perches. Birds in heavy moult may feed on ground by scuttling about after prey.

Breeding. Breeds mid-Apr to Jul, commencing early Mar in S of range, mid-May in N. Usually single-brooded. Territorial. Nest-site usually in open situation, may be used for several years; no nest, eggs laid on leaf litter or pine needles, on ground. Clutch 2 eggs, oval or elliptical, glossy, cream, pinkish-cream or white, blotched, marbled and spotted with brown, tawny, lilac, grey and purple, laid on consecutive days; replacement clutches sometimes laid if first lost; incubation usually by female during day, period generally c. 20 days; female threatened at nest-site may give distraction display from perch or on ground; eggs hatch asynchronously; chick semi-precocial, covered in golden-brown or yellowish-ochre down, fledge at c. 16 days but may remain dependent on adults for another 14 days.

Movements. Migratory, males generally moving before females. Begins arriving in N parts of range by mid-late Mar. Occasionally found N of normal breeding range, and perhaps also occurs N Bahamas. Post-breeding migration begins early Sept. Winters from S USA through Central America and West Indies to N South America. Vagrants recorded on St Martin, St Barthélemy and Barbuda. Adults tend to winter in Greater Antilles, immatures in Central & South America.

Status and Conservation. Not globally threatened. Generally common throughout North American breeding range, and apparently spreading N in some regions, with increases noted in Massachusetts and New York; common in winter in S parts of range, e.g. frequent in S half of Florida Peninsula. Common spring and autumn passage migrant through E Mexico; frequent winter visitor from SE Mexico to Honduras, though probably not common in Guatemala; common (Sept-May) in Hispaniola, uncommon (Sept-May) in Bahamas, Cuba and Jamaica and on Saba, rare (Sept-May) in Puerto Rico, Virgin Is and Cayman Is; widespread but uncommon passage migrant and winter visitor (Oct-Apr) in Costa Rica and Panama; perhaps rare winter visitor (late Nov to mid-Feb) in Colombia; casual winter visitor in Venezuela. On breeding grounds, predators of eggs include striped skunk (*Mephitis mephitis*).

Bibliography. Arvin (1981), Baieich & Harrison (1997), Bailey (1989), Barbour (1943), Below *et al.* (1996), Bent (1940), Biaggi (1983), Binford (1989), Bjorklund & Bjorklund (1983), Breckenridge (1982), Brush (1990), Buden (1993), Burcar *et al.* (1992), Cooper (1981), DeGraaf & Rappole (1995), Ferguson (1967), Fieken *et al.* (1967), Fjeldså & Krabbe (1990), Ganier (1964), Grant (1993), Hilty & Brown (1986), Holden (1964), Howell & Webb (1995a), Hoyt (1953), Johnsgard (1979), Kaufman (1996), Laurie (1984), Mengel (1976), Mengel & Jenkinson (1971), Mengel *et al.* (1972), Meyer de Schauensee & Phelps (1978), Monroe (1968), Muzny (1982), Orians & Paulson (1969), Paterson (1972b), Price *et al.* (1995), Raffaele *et al.* (1998), Ridgely & Gwynne (1989), Rohwer (1971), Rohwer & Butler (1977), Root (1988), Slud (1964), Stiles & Skutch (1989), Thompson & Ely (1989), Veit & Petersen (1993), Wetmore (1968a), Wetmore & Swales (1931).

27. Rufous Nightjar

Caprimulgus rufus

French: Engoulevent roux **German:** Rostnachtschwalbe **Spanish:** Chotacabras Colorado

Other common names: Ruddy Nightjar (*minimus*); St Lucia/St Lucien Nightjar (*otiosus*)

Taxonomy. *Caprimulgus rufus* Boddaert, 1783, Cayenne.

May form superspecies with *C. carolinensis*, with which has even been considered conspecific, but differs notably in both voice and morphology. Race *otiosus* has been considered a distinct species, on the basis of supposed sympatric breeding in N Venezuela; however, presence of this race in Venezuela now seems rather unlikely, as the relevant specimens were in poor condition and anyway do not appear to have matched *otiosus* well; also, differences from other races in vocalizations and plumage are minimal and do not appear to justify this split. Race *minimus* has also been considered a separate species, but again differences appear insufficient. Race *saltarius* initially thought to belong to *C. sericocaudatus*; subsequently found to be closer to present species, but thought to occur sympatrically with *rufus* and so raised to full species status; however, voice and morphometrics convincingly show it to belong within present species, where it is sometimes synonymized with *rufus*, being considered merely a grey plumage morph. Race *rufus* includes proposed forms *ornatus* and *cortapau*; nominate *rufus* includes proposed race *noctivigularis*. Recent sight records of present species from C Colombia, S Ecuador, Peru and C Brazil not yet subspecifically assigned; some of these may refer to as yet undescribed races. Five subspecies currently recognized.

Subspecies and Distribution.

C. r. minimus Griscom & Greenway, 1937 - S Costa Rica to N Colombia, N Venezuela and NW Trinidad (including Bocas Is).

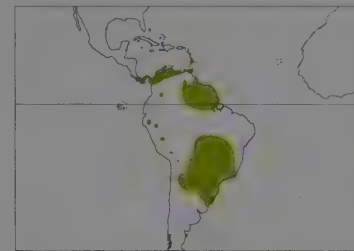
C. r. otiosus (Bangs, 1911) - NE St Lucia in Lesser Antilles.

C. r. rufus Boddaert, 1783 - S Venezuela E through the Guianas and NE Brazil.

C. r. rufus (Burmeister, 1856) - S Brazil, E Bolivia, Paraguay and NE Argentina.

C. r. saltarius Olog, 1979 - NW Argentina and possibly SE Bolivia.

Populations in C Colombia, S Ecuador, Peru and C Brazil of uncertain status and not yet assigned to race.



Descriptive notes. 25-30 cm; 1 male 88 g, female 89-98 g, 1 unsexed 95 g. Sexually dimorphic. Upperparts rufescent-brown, broadly streaked blackish-brown, with narrow and indistinct tawny-buff nuchal collar; lesser coverts dark brown, speckled rufous or tawny, rest of wing-coverts rufescent-brown, speckled rufous and buff and boldly spotted blackish-brown; scapulars boldly spotted blackish-brown; narrow white or buffish-white band around lower throat; underparts rufescent-brown, barred brown, speckled and spotted cinnamon, buff and white, becoming buff barred brown on undertail-coverts; both sexes lack white markings on

wings. Male has large white spot on inner webs of three outermost tail feathers, outer webs being tawny with black bars; female lacks white markings on tail. Iris dark brown, bill dusky with blackish tip, legs and feet brownish-flesh. Generally smaller and darker than *C. carolinensis*. Juvenile paler than adult, with crown, scapulars and some wing-coverts pale buff or whitish, distinctly spotted black. Racial variation includes overall coloration, size and colour of nuchal collar, and in males size of white tail spots. **Voice.** Nocturnal song of male is a loud "chuk, wee, wee, weeo" given from branches or rocks or sometimes from ground. Call is a guttural croak.

Habitat. Generally forest: rainforest, gallery forest, second-growth forest, open woodland and forest edge; also scrubland and savanna thickets and large suburban gardens. In Trinidad, typically in scrubland and deciduous woodland, and on St Lucia prefers arid brush country. Generally recorded from sea-level to 1000 m, but up to 1800 m in Colombia.

Food and Feeding. Feeds on insects. Forages by hawking or flycatching from low perches, often in forest interiors.

Breeding. Poorly known. Possibly breeds Jan-May in Panama, Jun on St Lucia, Feb-May in Trinidad, mid-Apr to May in Colombia, and Oct-Dec in N Argentina; no other published data available. Nest-site usually beneath vegetation or beside log; no nest, eggs laid on bare ground or leaf litter. Clutch 1-2 eggs, elliptical, creamy-white, blotched light brown and dull lilac; incubation usually by female during day; chick not described.

Movements. Poorly known; most populations may be sedentary. Race *rufus* partially migratory. S populations moving N after breeding season, possibly wintering (May-Aug) as far away as Venezuela. Race *saltarius* possibly also partially migratory.

Status and Conservation. Not globally threatened. Rare and local in S Costa Rica; locally fairly common on Pacific side of Panama, scarcer and more local on Caribbean side, occurring in Canal area only. Widely distributed and uncommon to fairly common throughout much of South America, where apparently not immediately endangered; fairly common in NW peninsula of Trinidad and on Bocas Is; widespread and not uncommon in some parts of St Lucia, especially in NE coastal areas; uncommon and infrequently recorded in Colombia; locally distributed in Venezuela, but present in Henri Pittier National Park; rare but possibly overlooked in Surinam; locally very common in Amazonian Brazil, common Apr-Oct in Mato Grosso but scarce in Rio Grande do Sul; fairly widespread in SW Bolivia; rare to uncommon in E Paraguay, and very common in NW Argentina. Loss of habitat through deforestation a potential threat in some regions, and on St Lucia eggs, chicks and possibly adults may be preyed by introduced mongooses (*Herpestes auripunctatus*) and rats (*Rattus*).

Bibliography. Babbs *et al.* (1988), Belton (1984), Canevari *et al.* (1991), Chebez (1994), Contreras *et al.* (1990), Dubs (1992), French (1991), Greenway (1967), Haverschmidt & Mees (1994), Hayes (1995), Hilty & Brown (1986), Keith (1997), Kiff (1975), Meyer de Schauensee & Phelps (1978), Nores & Yzurieta (1984), Olog (1979a), Oren & Parker (1997), de la Peña (1994), Raffaele *et al.* (1998), Ridgely & Gwynne (1989), Robbins & Parker (1997), do Rosário (1996), Schubart *et al.* (1965), Short (1975), Sick (1993, 1997), Slud (1964), Snyder (1966), Stiles & Skutch (1989), Stotz *et al.* (1996), Tostain *et al.* (1992), Wetmore (1968a), Wetmore & Phelps (1953).

28. Cuban Nightjar

Caprimulgus cubanensis

French: Engoulevent peut-on-voir **German:** Kubanachtschwalbe **Spanish:** Chotacabras Cubano

Other common names: (Greater) Antillean Nightjar (with *C. ekmani*)

Taxonomy. *Antrostomus Cubanensis* Lawrence, 1860. Ciénaga de Zapata and coast of Manzanillo, Cuba.

May form superspecies with *C. ekmani*, with which it was until recently considered conspecific, but notable differences in voice. Two subspecies recognized.

On following pages: 29. Hispaniolan Nightjar (*Caprimulgus ekmani*); 30. Tawny-collared Nightjar (*Caprimulgus salvini*); 31. Yucatan Nightjar (*Caprimulgus badius*); 32. Silky-tailed Nightjar (*Caprimulgus sericocaudatus*); 33. Buff-collared Nightjar (*Caprimulgus ridgwayi*); 34. Whip-poor-will (*Caprimulgus vociferus*); 35. Puerto Rican Nightjar (*Caprimulgus noctitherus*); 36. Dusky Nightjar (*Caprimulgus saturatus*).

Subspecies and Distribution.

C. c. cubanensis (Lawrence, 1860) - Cuba.

C. c. insulaepinorum Garrido, 1983 - I of Pines and Cayo Coco.



outermost tail feathers; female has narrow buff tips. Iris brown, bill blackish, legs and feet brownish. Differs from *C. ekmani* by less streaking on crown; also by broad pale buff throat band, and narrower white (male) or buff (female) tips to three outermost tail feathers. Immature plumages not described. Racial variation apparently clinal, with *insulaepinorum* smaller and darker. Voice. Song of male is a short, evenly pitched, trilled whistle, "terrrrrrrr"; a 4-syllable phrase, "gua bai ah ro". **Habitat.** Typically open woodland, but also favours edges of swampland and rivers. On Isle of Pines, also dense woodland and scrubland.

Food and Feeding. Feeds on insects. Foraging methods not described.

Breeding. Poorly documented. Breeds Mar-Jul. Nest-site in dense scrub or thicket at edge of clearing; no nest, eggs laid on leaf litter on ground. Clutch 1-2 eggs, elliptical, dull white often tinged pinkish-buff, marked and spotted brown, brownish-buff and greyish-purple; both sexes incubate; adults threatened at nest-site may perform distraction display; chick not described.

Movements. None recorded. Sedentary.

Status and Conservation. Not globally threatened. Poorly known, with few data available. Occurs throughout Cuba, where possibly locally common. On Isle of Pines, first reported in dense woodland S of Ciénaga de Lanier in 1905 and still apparently commoner in that region and the S than elsewhere on the island. Potential threats to breeding birds include the introduced small mongoose (*Herpestes auro-punctatus*).

Bibliography. Alayón (1985), Anon. (1998a), Balát & González (1982), Barbour (1943), Bond (1934, 1985), García (1985), Garrido (1983), Garrido & Reynard (1994, 1998), Gundlach (1873), Raffaele *et al.* (1998), Stotz *et al.* (1996), Vaurie (1957).

29. Hispaniolan Nightjar

Caprimulgus ekmani

French: Engoulevent d'Hispaniola

Spanish: Chotacabras de la Española

German: Hispaniolanachtschwalbe

Other common names: (Greater) Antillean Nightjar (with *C. cubanensis*)

Taxonomy. *Antrostomus ekmani* Lönnberg, 1929, near Jérémie, Haiti.

May form superspecies with *C. cubanensis*, with which it was until recently considered conspecific, but notable differences in voice. Monotypic.

Distribution. Hispaniola.



broader white (male) or buff (female) tips to three outermost tail feathers. Juvenile very dark, almost blackish. Voice. Song of male is a short "clik" or "tuc" followed by a trilled whistle that rises in pitch: "tuc, terrreo". Calls include soft "quat" and deep, crow-like "gaaw" sounds.

Habitat. Typically pine forests, from possibly sea-level to 1500 m.

Food and Feeding. Feeds on insects. Foraging methods not described.

Breeding. Breeding habits almost entirely undocumented. Breeds Apr-Jul; almost fully grown chicks in mid-Aug. No nest, eggs laid on ground; one brood of two chicks found on overgrown forest path. Clutch generally 2 eggs, pale greenish-white, spotted brown; chick not described.

Movements. None recorded. Sedentary.

Status and Conservation. Not globally threatened. Locally widespread in suitable habitat throughout Haiti and Dominican Republic, though probably not common at any locality; fairly common in Sierra de Bahoruco National Park.

Bibliography. Anon. (1998a), Bond (1985), Dod (1987), Garrido & Reynard (1994, 1998), del Hoyo (1999), Lönnberg (1929), Raffaele *et al.* (1998), Stotz *et al.* (1996), Wetmore & Swales (1931).

30. Tawny-collared Nightjar

Caprimulgus salvini

French: Engoulevent de Salvín

German: Salvinnachtschwalbe

Spanish: Chotacabras Ticuer

Other common names: Salvín's Chuck-will, Chipwillow

Taxonomy. *Caprimulgus salvini* Hartert, 1892, no locality = Mirador, Veracruz, Mexico.

Forms superspecies with *C. badius* and *C. sericocaudatus*, all three sometimes being considered conspecific. Monotypic.

Distribution. E Mexico.

Descriptive notes. 23-25.5 cm. Sexually dimorphic. Upperparts blackish-brown boldly streaked and spotted blackish, with indistinct tawny or buff nuchal collar; wing-coverts blackish-brown,

Descriptive notes. 25-29.5 cm; male 68-80 g, female 50-70 g. Sexually dimorphic. Upperparts blackish-brown, speckled greyish-brown, greyish-white and pale buff; crown broadly streaked blackish, no nuchal collar; wing-coverts blackish-brown, speckled and spotted pale buff; scapulars buffish-white, speckled brown and boldly spotted blackish-brown; buffish-white submoustachial stripe and broad pale buff band around lower throat; underparts buffish-white, speckled and spotted blackish-brown, becoming buff vermiculated brown on undertail-coverts; both sexes lack white markings on wings. Male has white tips to three



to three outermost tail feathers. Immature plumages not described. Voice. Song of male is a rapid "chip, willow", "yip, willow" or "chip, wow"; sings from perches at dusk and dawn.

Habitat. Lowland semi-deserts and dry, open woodland with scrub; occasionally also farmland and fields, thickets, forest edges and clearings. Recorded from sea-level to 500 m.

Food and Feeding. Feeds on insects. Forages from perches and possibly from ground.

Breeding. Poorly documented. Breeds Apr-Aug. Clutch 2 eggs, whitish with brown and grey markings; chick not described.

Movements. Generally sedentary, although occasionally undertakes local movements outside breeding season (Dec-Feb) to S Veracruz and N Oaxaca. A skin from N Nicaragua probably refers to this species, although sometimes referred to *C. badius*.

Status and Conservation. Not globally threatened. Generally confined to woodland and scrubland in E Mexico, where considered a common to fairly common breeding bird in lowlands. Status uncertain in SE Mexico, with record from NW Chiapas

Bibliography. Anon. (1998a), Binford (1989), Eisenmann (1955), Hardy & Straneck (1989), Howell & Webb (1995a), Lowery & Dalquest (1951), Pierson (1986), Stotz *et al.* (1996).

31. Yucatan Nightjar

Caprimulgus badius

French: Engoulevent maya

Spanish: Chotacabras Guatemalteco

German: Guatemalanachtschwalbe

Other common names: Yucatan Tawny-collared Nightjar

Taxonomy. *Antrostomus badius* Bangs and Peck, 1908, Toledo district, Belize.

Forms superspecies with *C. salvini* and *C. sericocaudatus*, all three sometimes being considered conspecific. Present species has alternatively been treated as a race of one or other of the above species, although vocally it may be closest to *C. rufus*. Monotypic.

Distribution. Yucatán Peninsula of SE Mexico; also Cozumel I.



Descriptive notes. 25-25.5 cm; 1 male 65.5 g, female 51-56 g. Sexually dimorphic. Upperparts greyish-brown, spotted and speckled greyish-white and heavily spotted and streaked blackish-brown; broad tawny-buff or rufescent nuchal collar; wing-coverts greyish-brown, spotted and speckled greyish-white, cinnamon, buff and tawny; broad buffish-white band around lower throat; underparts brownish heavily spotted white, becoming buff barred brown on undertail-coverts; both sexes lack white markings on wings. Male has broad white tips to three outermost tail feathers; female has narrow tawny-buff tips. Iris dark

brown, bill blackish, legs and feet blackish-brown. Generally paler than *C. salvini*, with nuchal collar paler and broader. Smaller and paler than *C. sericocaudatus*. Immature plumages not described. Voice. Song of male is an undulating "whee, wee-a, wee-a" or "ree-o, ree, ree", similar to that of *C. sericocaudatus*. Sings mainly at dusk and dawn. Call is a series of "chuk" notes.

Habitat. Mainly open, lowland woods and forest, and also forest edge.

Food and Feeding. Feeds on insects. Foraging methods not described.

Breeding. Almost entirely undocumented. Possibly breeds Apr-Aug. Clutch 2 eggs, elliptical, white, sparsely flecked and blotched brown and purplish-grey; chick not described.

Movements. Generally sedentary, though some S movement outside breeding season; recorded Dec-Feb in Belize. Also claimed to occur in Caribbean lowlands of Guatemala, N Nicaragua and Half Moon Cay.

Status and Conservation. Not globally threatened. In 1950's considered extremely rare and confined to deciduous forests, though probably under-recorded; currently regarded as a fairly common to common breeding bird locally, occurring in Yucatán, Quintana Roo and much of Campeche, and also on Cozumel I. Possibly an extremely rare resident in Guatemala, though validity of records often questioned; recently heard in Campeche, only 11 km from Mexican border with Guatemala. Single possible record from N Nicaragua, a museum specimen taken Apr 1917, but this is usually attributed to *C. salvini*.

Bibliography. Anon. (1998a), Davis (1979a), Gómez de Silva (1998), Hardy & Straneck (1989), Howell (1997), Howell & Webb (1995a), Klaas (1968), Land (1970), Paynter (1955), Pierson (1986), Russell (1964), Stotz *et al.* (1996), Valiely & Whitman (1997).

32. Silky-tailed Nightjar

Caprimulgus sericocaudatus

French: Engoulevent à queue de soie

Spanish: Chotacabras Coladeseda

German: Seidennachtschwalbe

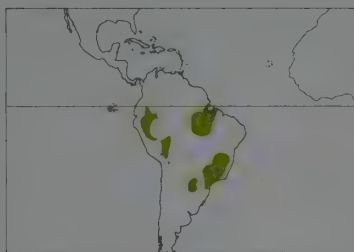
Taxonomy. *Antrostomus serico-caudatus* [sic] Cassin, 1849, Rio de Janeiro, Brazil.

Forms superspecies with *C. salvini* and *C. badius*, all three sometimes being considered conspecific. *C. rufus saltarius* initially thought to belong in present species, but might alternatively be separate species or merely colour morph of *C. r. rutilus*. Two subspecies recognized.

Subspecies and Distribution.

C. s. mengeli Dickerman, 1975 - N Brazil, N Peru and NW Bolivia.

C. s. sericocaudatus (Cassin, 1849) - SE Brazil, E Paraguay and extreme NE Argentina.



Descriptive notes. 24-30 cm; male 62-83 g, female 53-66 g. Sexually dimorphic. Upperparts dark greyish-brown, broadly streaked and spotted blackish-brown; very broad but indistinct tawny-buff nuchal collar; wing-coverts brown, spotted buff and cinnamon; large buff or buffish-white patch on lower throat; underparts brown, boldly spotted whitish; both sexes lack white markings on wings. Male has whitish tips to three outermost tail feathers; female has narrow buff tips. Iris dark brown, bill blackish, legs and feet blackish-brown. Larger than *C. salvini*, with narrower white tips to three outermost tail feathers. Larger and generally

darker than *C. badius*, with a broader but less conspicuous rufescent nuchal collar; male has narrower white tips to three outermost tail feathers. Immature similar to adult, but has narrower white or buff tips to three outermost tail feathers. Race *mengeli* smaller and darker. VOICE. Song of male is an undulating "doh, wheo, eeo" given from low perches, mainly at dusk and dawn. Calls include treble-noted "gawrr, a gawrr", or longer "gawrr, a gawrr, a gawrr". Song of race *mengeli* is more melodious, drawn out and higher pitched: "doh, wheeo, wheeo".

Habitat. Mainly forest, in clearings, especially where there are thickets, bamboo understorey or second-growth, and along forest edge. Nominant race occurs in subtropical evergreen forest; *mengeli* prefers tropical rainforest.

Food and Feeding. Feeds on beetles, crickets, grasshoppers and ants. Foraging methods not described.

Breeding. Almost entirely undocumented. No nest, eggs laid on leaf litter on ground. Eggs elliptical; chick not described.

Movements. None documented. Sedentary.

Status and Conservation. Not globally threatened. Generally uncommon and little known. Widely but sparsely distributed in Peru; widespread and possibly rare to fairly common in E Paraguay; locally uncommon to fairly common in NE Argentina. Loss of habitat through deforestation possibly poses greatest threat in many regions.

Bibliography. Canevari *et al.* (1991), Chebez (1994), Chebez *et al.* (1988), Davis *et al.* (1994), Dickerman (1975), Hardy & Straneck (1989), Hayes (1995), Madroño & Esquivel (1997), Madroño *et al.* (1997), Narosky & Yzurieta (1993), Parker *et al.* (1982), Partridge (1956), de la Peña (1994), Remsen & Traylor (1989), Saibene *et al.* (1996), Schulenberg & Remsen (1982), Sick (1993, 1997), Storer (1989), Stotz *et al.* (1996), Traylor (1958a).

33. Buff-collared Nightjar *Caprimulgus ridgwayi*

French: Engoulevent de Ridgway **Spanish:** Chotacabras Tucuchillo

German: Brauhals-Nachtschwalbe

Other common names: Ridgway's Whip-poor-will, Cookachea, Tucuchillo

Taxonomy. *Antrastomus ridgwayi* Nelson, 1897, Guerrero, Mexico.

Two subspecies recognized.

Subspecies and Distribution.

C. r. ridgwayi (Nelson, 1897) - extreme SW USA and W & S Mexico.

C. r. troglodytes Griscom, 1930 - C Guatemala, C Honduras and C Nicaragua.



Descriptive notes. 21.5-24.5 cm; male 45-54 g, female 45-53 g. Sexually dimorphic. Upperparts greyish-brown streaked blackish-brown; crown boldly spotted blackish-brown; broad tawny or buff nuchal collar; wing-coverts greyish-brown, streaked and spotted blackish-brown, and speckled and spotted greyish-buff and buff; scapulars greyish-brown, boldly spotted blackish-brown edged tawny or cinnamon; narrow buffish-white supercilium and moustachial stripe; broad buffish-white band around lower throat; underparts greyish-brown tinged cinnamon, streaked and speckled brown, becoming pale buff barred brown on belly and

flanks; both sexes lack white markings on wings. Male has broad white tips to three outermost tail feathers; female has narrow buffish tips. Iris brown, bill blackish, legs and feet brownish. Generally paler than *C. vociferus*, with broader tawny-buff nuchal collar. Immature similar to adult. Race *troglodytes* is smaller and often has scapulars more boldly spotted cinnamon or tawny. VOICE. Song of male is an accelerating "cuk, cuk, cuk, cuk, cuk, chuka-cheea" or "tok, tok, tek, tek, tek, teeka-teea", ascending slightly in pitch. Sings from ground, rocks or low perches. Call is a descending series of deep, guttural "tuk" notes.

Habitat. Typically rocky, arid or semi-arid areas, in deciduous forest, mixed forest of pine and oak, second-growth forest, woodland, scrubland, fields and thickets. Also on rock-strewn hillsides with scattered vegetation. Tends to avoid areas where rocks and vegetation are absent. Recorded from sea-level to 2400 m.

Food and Feeding. Feeds on beetles, moths and other insects. Hunts by making short flycatching sallies from ground or elevated perches, including tree branches and cliff faces; also forages low over open ground.

Breeding. Poorly documented. Possibly breeds Mar-Aug in SW USA and Mexico. Territorial. Nest-site often partly shaded by vegetation; no nest, eggs laid on leaf litter or rocky ground. Clutch 2 eggs, elliptical, buff, blotched brown and lilac; chick semi-precocial; adults flushed from nest-site may perform injury-feigning distraction display.

Movements. Poorly known. Nominant race sedentary in S of range, partly migratory in N, small numbers summering (May-Aug) in SE Arizona and SW New Mexico. Race *troglodytes* largely sedentary.

Status and Conservation. Not globally threatened. Possibly undergoing a slight range expansion to N. Probably rare summer visitor in SW USA, where first reported in 1958 and recorded only from Pima, Santa Cruz, Pinal and Cochise counties in SE Arizona and from Hidalgo and Dona Ana counties in New Mexico. Collecting of specimens banned from US locations; proposed as Species of Concern by Arizona Game and Fish Department, and since Jan 1975 listed as endangered in New Mexico by New Mexico Department of Game and Fish. Fairly common to common in Mexico, mainly on W side from Sonora and Chihuahua S to Oaxaca; local in C & S Veracruz and Chiapas. Major threat in some regions, especially in E of Mexican range, probably loss of habitat due to land

clearance for cattle rearing. Uncommon resident in Motagua Valley, C Guatemala, and rare to uncommon in Honduras. Potential predators include birds of prey, owls (Strigidae) and bobcats (*Lynx rufus*), while eggs and chicks might be taken by snakes, skunks (Mustelidae), foxes (Canidae), ringtails (*Bassaris astutus*) and white-nosed coatis (*Nasua narica*). In some regions, small numbers are occasionally killed by traffic on roads.

Bibliography. Álvarez del Toro (1949), Baicich & Harrison (1997), Binford (1989), Bowers & Dunning (1997), Davis (1957), Griscom (1929, 1930), Howell & Webb (1990, 1995a), Jenkinson & Mengel (1970), Johnston & Hardy (1959), Kaufman (1996), Land (1970), Levy (1962), Monroe (1968), Nicol & Arnott (1974), Pyle (1995), Rowley (1962), Schaldach (1963), Short (1974), Stotz *et al.* (1996), Sutton (1951a).

34. Whip-poor-will *Caprimulgus vociferus*

French: Engoulevent bois-pourri

Spanish: Chotacabras Cuerporruín

German: Schwarzkehl-Nachtschwalbe

Other common names: Northern Whip-poor-will (*vociferus*); Mexican Whip-poor-will (*arizonae* group)

Taxonomy. *Caprimulgus vociferus* Wilson, 1812, Pennsylvania.

May form superspecies with *C. noctitherus*, with which formerly considered conspecific. Differences in vocalizations suggest that Central American races may be better split from nominate, as *C. arizonae*. Six subspecies currently recognized.

Subspecies and Distribution.

C. v. vociferus Wilson, 1812 - SC & SE Canada and EC & E USA; winters from SC & SE USA through Central America.

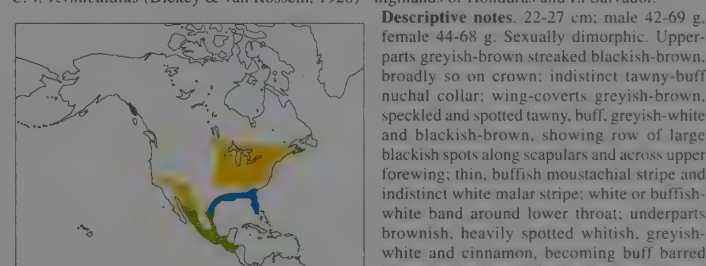
C. v. arizonae (Brewster, 1881) - SW USA S to C Mexico; winters in C Mexico.

C. v. setosus van Rossem, 1934 - E Mexico.

C. v. oaxacae (Nelson, 1900) - SW Mexico.

C. v. chiapensis (Nelson, 1900) - SE Mexico and highlands of Guatemala.

C. v. vermiculatus (Dickey & van Rossem, 1928) - highlands of Honduras and El Salvador.



Descriptive notes. 22-27 cm; male 42-69 g, female 44-68 g. Sexually dimorphic. Upperparts greyish-brown streaked blackish-brown, broadly so on crown; indistinct tawny-buff nuchal collar; wing-coverts greyish-brown, speckled and spotted tawny, buff, greyish-white and blackish-brown, showing row of large blackish spots along scapulars and across upper forewing; thin, buffish moustachial stripe and indistinct white malar stripe; white or buffish-white band around lower throat; underparts brownish, heavily spotted whitish, greyish-white and cinnamon, becoming buff barred brown on belly and flanks; both sexes lack

white markings on wings. Male has broad white tips to three outermost tail feathers; female has narrow buff tips. Iris dark brown, bill dark brown or blackish, legs and feet brownish. Smaller than *C. carolinensis* with less apparent spotting; male has much more white on outermost tail feathers; female has more readily apparent buff tips to tail feathers. Darker than *C. ridgwayi*, with narrower, less distinct tawny nuchal collar. Much paler and more uniformly patterned than *C. saturatus*. Larger and paler than *C. noctitherus*. Immature similar to adult but often buffier. Races vary somewhat in overall coloration and in size. VOICE. Song of male is a whistled "whip, pr-will" or "whip, pr-weee", last note usually rising in pitch at end, and is often preceded by or interspersed with several short, sharp "quirt" notes; song of W race *arizonae* is more liquid and melodious. Sings from perches and ground, mainly at dusk and dawn and on moonlit nights. Flight/contact call of race *arizonae* is repetitive "hu-whip"; alarm/distress calls include short "cook", soft "whip-will" or "whip" notes; other calls include soft "coo" or "cook" notes, melodious "coo-eu" or "coo-eu-ah" calls, guttural chuckles, "cur, cur, cur" and soft "quirt-quirt"; guttural hissing sounds are given during threat/defence displays.

Habitat. All types of forest and open woodland, especially of oak or mixed pine and oak. Tolerates both arid and more humid conditions, from lowlands to montane altitudes. Also in suburban habitats, and on migration in coastal scrub. Race *arizonae* occurs in lowland oak woods and mixed forest of oak and sycamore, in highland woods of yellow pine, aspen or Douglas fir (*Pseudotsuga menziesii*) and in montane spruce forest. Recorded from sea-level to 3000 m.

Food and Feeding. Feeds on moths, beetles, grasshoppers, crickets, mosquitoes, caddisflies, locusts, ants and possibly worms. Forages by making short sallies from perches or hunts in more prolonged flights, in clearings, open spaces and among trees. Often feeds near running water. May occasionally feed on ground, and may ingest grit to aid digestion.

Breeding. Breeds May-Jul in North America, mid-Mar to Jul in Mexico, and possibly late Feb to May in El Salvador; breeding often synchronized with moon phases. Often double-brooded, beginning second clutch c. 33 days after first, male apparently brooding chicks of first while female attends second. Territorial. Nest-site in clearing or glade, along edge of trees or wood, or beneath vegetation, in more arid country (race *arizonae*) also below rocks, in rocky, forested ravine, or on outcrop, escarpment or steep hillside: same site may be used for several years; no nest, eggs laid on leaf litter on ground, often near or beside fallen log. Clutch 1-2 eggs, elliptical, slightly glossy, white or pale cream, and unmarked or faintly marked pinkish and brownish or blotched and irregularly spotted brown, purple and lilac, laid on consecutive days; incubation begins with first egg, usually by female during day, with change-over at dusk, shared by both sexes during night. Female taking over again before dawn; incubation period generally 19-21 days; chick covered in cinnamon, pale brown or buff down, fading to yellowish-tan within few days; adults threatened at nest-site perform distraction display; chicks fledge after c. 15 days, usually independent after c. 30 days.

Movements. Nominant race migratory, arriving on S breeding grounds by late Mar and on N by early May. Possibly casual visitor to SW & C Canada and accidental to SE Alaska. Probably departs from breeding grounds Sept-Nov and winters in lowlands of South Carolina and Gulf States, S through E Mexico (Sept-Apr) to Guatemala, S Belize, El Salvador and Honduras. Also a casual winter visitor in S California, W Cuba, Jamaica, Costa Rica (perhaps rare on Pacific slope mid-Nov to late Mar) and W Panama (possibly 2 records, W Chiriquí), and occasionally winters along E coast of USA as far N as New Jersey. Race *arizonae* migratory, arriving on breeding grounds by late Apr and departing again by late Sept, though perhaps only an altitudinal migrant in parts of Mexican range. Casual visitor to Baja California. Generally winters in C Mexico. Other populations may be largely sedentary.

Status and Conservation. Not globally threatened. Generally very common to locally abundant throughout much of range, though decreasing in many regions in N. Declining in some areas in

Ontario: locally fairly common in Massachusetts but numbers falling; in Connecticut, common before 1920's but steady decline after 1930's, now considered locally rare to uncommon and designated as Species of Special Concern. Slowly declining in Ohio; becoming less common in Vermont; local decreases noted in W Virginia since 1950's and now absent from some regions; declined in Michigan and New York State; in Pennsylvania, decreased in last 50 years and now disappeared from some regions. Fairly common to common throughout much of C Mexico, numbers increasing in non-breeding season with arrival of migrants from farther N, although birds from North American populations apparently winter more to E. Fairly common in Guatemalan highlands; rare resident in El Salvador, although N migrants are common in winter; very rare and casual winter visitor to Pacific side of Costa Rica; extremely rare winter visitor to W Chiriquí highlands, W Panama. In N breeding populations, reasons for decline include loss of habitat to agriculture and urbanization, industrial pollution and use of insecticides which may affect food availability, increasing road traffic, predation by domestic cats, and disturbance at nest-sites by people and dogs.

Bibliography. Andrie & Carroll (1992), Babcock (1975), Baicich & Harrison (1997), Bent (1940), Bevier (1994), Binford (1989), Bjorklund & Bjorklund (1983), Blackford (1953), Bolles (1912), Brauning (1992), Bruce (1973), Coale (1920), Cooper (1981, 1982), Cyr (1995g), Dean *et al.* (1995), Dearborn (1907), DeGraaf & Rappole (1995), DuBois (1911), Dyer (1977), Ehrlich *et al.* (1992), Fowle & Fowle (1954), Hall (1983), Hersey (1923), Hickey (1993), Howell & Webb (1995a), Johnsgard (1979), Kaufman (1996), Kent & Vane (1958), Kilham (1957), Laughlin & Kibbe (1985), Lowery & Dalquest (1951), McPeck (1984), Mills (1985, 1986, 1987), Monroe (1968), North (1996), Orians & Paulson (1969), Peterjohn (1989), Pitocchelli (1995), Price *et al.* (1995), Rauth (1979), Raynor (1941), Ridgely & Gwynne (1989), Root (1988), Rowley (1966, 1984), Slud (1964), Small, A. (1994), Small, P.E. & Emanuel (1996), Stiles & Skutch (1989), Stotz *et al.* (1996), Sutton (1941b), Thurber *et al.* (1987), Tuttle (1911), Urban (1959), Wetmore (1968a), Zeranski & Baptist (1990).

35. Puerto Rican Nightjar

Caprimulgus noctitherus

French: Engoulevent de Porto Rico

Spanish: Chotacabras Portorriqueño

German: Puerto-Rico-Nachtschwalbe

Taxonomy. *Setochalcis noctitherus* Wetmore, 1919, Bayamón, Puerto Rico.

May form superspecies with *C. vociferus*, with which formerly considered conspecific. Monotypic. **Distribution.** SW Puerto Rico.



Descriptive notes. 22-22.5 cm; unsexed 35-37 g. Sexually dimorphic, though not strongly so. Upperparts greyish-brown tinged rufous and streaked blackish-brown, broadly so on crown; indistinct tawny-buff nuchal collar; wing-coverts greyish-brown, speckled and spotted buff, tawny and greyish-white, showing row of large blackish spots across upper forewing and along scapulars; white or buffish-white band around lower throat; underparts brownish, heavily spotted greyish-white and cinnamon, becoming buff barred brown on belly and flanks; both sexes lack white markings on wings. Male has broad white tips to three outermost tail feathers; female has narrow, buffish tips. Iris dark brown, bill blackish, legs and feet blackish-brown. Immature paler than adult. **Voice.** Song of male is a rapid series of short, liquid whistles, "whlip, whlip, whlip, whlip, whlip", often preceded by faint "quert" notes. Sings from perches throughout night. Calls include short growls, "quert" and "gaw" notes, and soft, clucking or guttural sounds; gives guttural hissing sounds during threat/defence displays.

Habitat. Typically semi-deciduous forest with hardwood trees and little or no ground vegetation, usually on dry, limestone soils; also dry, open secondary growth with scrub, xeric or dry scrubland, open scrub forest, and forest with tangled, thorny undergrowth. Occasionally frequents plantations of *Eucalyptus robusta*. Avoids riparian forest, and is found in disturbed areas only where canopy is still intact. A lowland species, recorded from sea-level to 230 m.

Food and Feeding. Feeds on beetles, moths and other insects. Forages by making flycatching sallies from perches and hunts beneath tree canopy. Smaller prey items are probably consumed in flight, but larger insects are carried in bill back to perch where they are shaken and swallowed. Also feeds on insects attracted to artificial lights, where birds often fly through insect swarms with gapes open, or land on ground with wings outstretched, to pick up beetles. Immature birds may forage by making short sallies from ground, and may feed on ground itself.

Breeding. Breeds late Feb-Jul (mainly Apr-Jun), apparently influenced by moon phase. Possibly double-brooded. Territorial. Nest-site usually partly shaded, beneath scrub vegetation in woodland

where canopy height 4-6 m, or at base of small tree; no nest, eggs laid on leaf litter on ground. Clutch 1-2 eggs, elliptical, buffish-brown, blotched and spotted purple, with markings denser around blunt end; incubation by both sexes, male incubating more than female during day, period generally 18-21 days; eggs hatch asynchronously, chick semi-precocial, covered in reddish-buff or cinnamon down, generally brooded by male, can fly short distances after c. 14 days; adults threatened at nest-site perform injury-feigning distraction display.

Movements. None recorded. Sedentary.

Status and Conservation. CRITICALLY ENDANGERED. Restricted-range species; present in Puerto Rico and the Virgin Islands EBA. Long thought to be extinct until rediscovered in 1961. Population in 1984 estimated at 670-800 pairs: Guánica forest c. 324 pairs (c. 1 pair per 8 ha above 75 m and c. 1 pair per 18-8 ha between 25-75 m), Susúa forest c. 68 pairs (1 pair per 8-1 ha N of Carretera del Bosque and 1 pair per 24-5 ha S of Carretera del Bosque), and Guayanilla hills c. 263 singing males. Studies in 1985-87, 1989-90 and 1992 produced total of 712 singing males in 9839 ha: 347 in Guánica area, 177 in Susúa-Maricao area and 188 in Guayanilla area. Current population possibly numbers 1400-2000 individuals in c. 10,000 ha of coastal dry and cordillera forest in SW Puerto Rico. Loss of habitat through deforestation is a possible reason for current, restricted range; potential predators include feral cats and introduced mongooses (*Herpestes erpuncatus*).

Bibliography. Anon. (1998a), Binggi (1983), Bond (1985), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Díaz (1983), Greenway (1967), Johnson (1988), Kepler & Kepler (1973), King (1978/79), Noble (1988), Noble *et al.* (1986a, 1986b), Raffaele (1989), Raffaele *et al.* (1998), Reynard (1962), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Vilella (1989, 1990, 1995a, 1995b), Vilella & Zwank (1987, 1988, 1993a, 1993b), Wetmore (1919).

36. Dusky Nightjar

Caprimulgus saturatus

French: Engoulevent montagnard

Spanish: Chotacabras Fuliginoso

German: Bergnachtschwalbe

Other common names: Sooty Nightjar

Taxonomy. *Antrostomus saturatus* Salvin, 1870, Volcán de Chiriquí, Panama. Monotypic.

Distribution. C highlands of Costa Rica to W Panama.



Descriptive notes. 21-25 cm; 1 male 53 g, 1 female 51 g. Sexually dimorphic. Upperparts and wing-coverts blackish-brown, heavily spotted tawny and buff, no nuchal collar; indistinct pale buffish band around lower throat; underparts blackish-brown heavily spotted tawny, becoming dark buff barred brown and spotted whitish on belly and flanks; female often paler and more rufous than male; both sexes lack white markings on wings. Male has broad white tips to three outermost tail feathers; female has narrow tawny-buff tips. Iris dark brown, bill blackish, legs and feet greyish or dark brownish. Immature similar to adult

but paler and more rufous. **Voice.** Song of male is a trilled whistle, "prurrrrr, prurree" or "prurrrrr, prurwhip", first note evenly pitched, second rising in pitch at end. Sings from perches and possibly also from ground, mainly at dusk and dawn. Flight calls are scratchy "wheer" sounds.

Habitat. Mainly montane forest or woodland, in clearings and areas of second growth or along forest edges; also upland pastures with scattered trees. Recorded at 1500-3100 m.

Food and Feeding. Feeds on moths and beetles. Forages from perches, hunting over open spaces in or near woods and forests.

Breeding. Poorly known. Possibly breeds Feb-Apr (juveniles found in Apr). Nest-site in clearing with scattered trees, often among tall grass and ferns; no nest, egg laid on leaf litter or grass, on ground. Clutch possibly 1 egg, elliptical, dull or glossy white; chick not described.

Movements. None recorded. Sedentary.

Status and Conservation. Not globally threatened. Restricted-range species; present in Costa Rica and Panama Highlands EBA. Locally common and widespread in C highlands of Costa Rica, uncommon in forested highlands of W Chiriquí, W Panama. Present in Volcán Poás National Park and Monteverde Biological Reserve (Costa Rica).

Bibliography. Anon. (1998a), Blake (1958), Hernández-Baños *et al.* (1995), Marin & Schmitt (1991), Ridgely & Gwynne (1989), Slud (1964), Stattersfield *et al.* (1998), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968a).

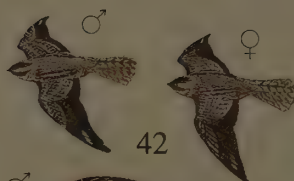
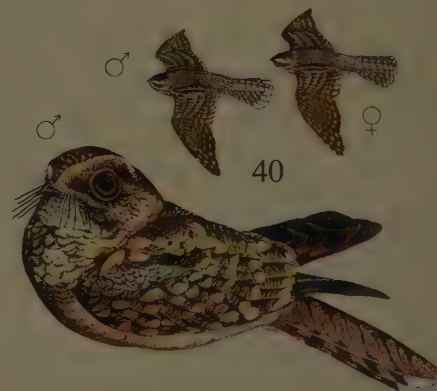
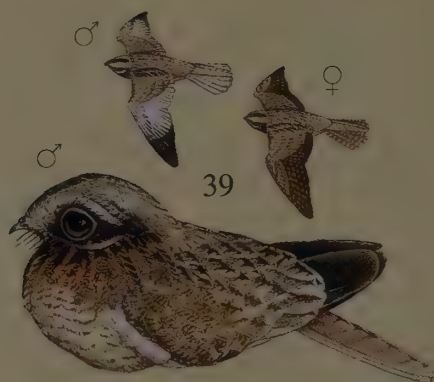


PLATE 30

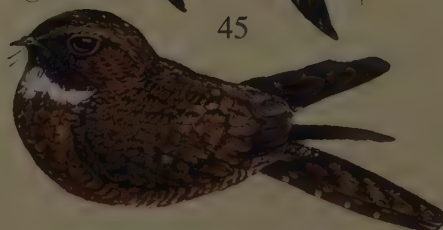
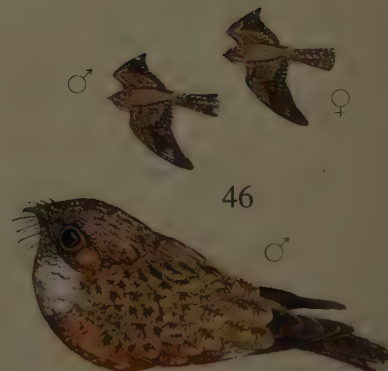
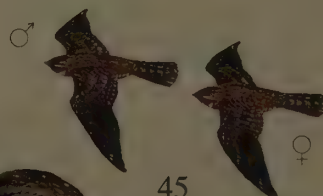
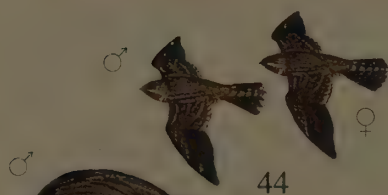
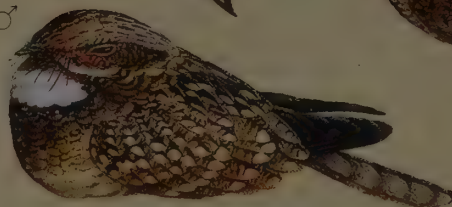
inches 4
cm 10



37



41



37. Band-winged Nightjar

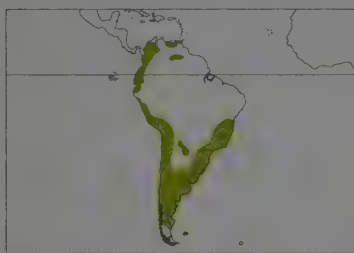
Caprimulgus longirostris

French: Engoulevent à miroir **German:** Spiegelnachtschwalbe **Spanish:** Chotacabras Ñañarca
Other common names: Rufous-naped Nightjar (*ruficervix*)

Taxonomy. *Caprimulgus longirostris* Bonaparte, 1825, South America. Race *ruficervix* has sometimes been treated as a separate species, but geographical variation in voice remains too poorly known to provide a clear picture of the relationships. Seven subspecies currently recognized.

Subspecies and Distribution.

C. l. ruficervix (P. L. Sclater, 1866) - W & N Venezuela, W Colombia and Ecuador.
C. l. roraimae (Chapman, 1929) - Pantepui of S Venezuela.
C. l. atripunctatus (Chapman, 1923) - C & S Peru, C & SW Bolivia, NW Argentina and N Chile.
C. l. decussatus Tschudi, 1844 - SW Peru and extreme N Chile.
C. l. bifasciatus Gould, 1837 - Chile and W Argentina.
C. l. longirostris Bonaparte, 1825 - SE Brazil, NW & C Paraguay, NE Argentina and Uruguay.
C. l. patagonicus Olog, 1962 - C & S Argentina.



Descriptive notes. 20-27 cm; male 29-50 g, female 32-71 g. Sexually dimorphic. Upperparts greyish-brown streaked blackish-brown, or blackish-brown mottled tawny, buff and greyish-white; broad tawny or buffish nuchal collar; wing-coverts greyish-brown or blackish-brown, boldly spotted buff, pale buff or greyish-buff; scapulars blackish-brown, boldly spotted buff; a large white (male) or buffish (female) patch around lower throat; underparts brownish, barred and spotted buff, becoming buff barred brown on belly and flanks. Male has white band across four outermost primaries and broad white tips to three or four outermost.

most tail feathers, with white bar across upper half of inner webs; female has narrow buffish or buffish-white wing band, and either lacks white on tail or has indistinct whitish spot on inner webs of one or two outermost tail feathers. Iris brown, bill blackish, legs and feet blackish-brown. Larger and somewhat paler than *C. whitelyi*, which lacks a nuchal collar and has different wing and tail markings. Immature similar to adult but plainer, with narrow tawny wing bands. Two racial groups recognized: blackish and spotted forms (*ruficervix*, *roraimae*, *atripunctatus*) and greyish-brown and streaked forms (*decussatus*, *bifasciatus*, *longirostris*, *patagonicus*); some races differ slightly in size and all are extremely variable in coloration and markings. **VOICE.** Song of male is a repetitive, high-pitched whistle, "seeeeeert", that can be quite variable. Singing from low perches or ground, mainly at dusk and dawn. Flight calls are thin, high-pitched "cheet" notes, also nasal "tchree-ee", e.g. when flushed.

Habitat. Typically inhabits forest edges, woodland borders, open woodland, clearings, arid bush and campos. Also occurs in a wide variety of other habitats, including open areas with low vegetation, shrubby páramos, puna grassland, deserts and stony semi-deserts, steppe country and grassy slopes in semi-arid elfin forest; sometimes found in towns and cities. Recorded from sea-level up to 4200 m.

Food and Feeding. Feeds on moths, beetles and termites. Forages by making short sallies from ground or low perches. Also feeds on insects attracted to artificial lights.

Breeding. Possibly breeds Feb-Sept in W Venezuela, Mar-Nov in Colombia, up to and from late Jul in Ecuador, from Nov in Chile and C Argentina, and Sept-Oct in SE Brazil. Nest-site located among regenerating vegetation on burnt ground, beside road, at cliff base, among vegetation in semi-arid country, or on roof of old building; no nest, eggs laid on bare ground, leaf litter or bare rock. Clutch 1-2 eggs, elliptical or subelliptical, pinkish, creamy-pink or whitish, speckled and scrawled brown, lilac and grey, or unmarked; chick not described.

Movements. Poorly understood. Nominate race may be sedentary in N of range, migratory in S, as possibly this race occurs in Paraguay late May to late Aug as a probable migrant from S. No movements documented for subspecies *ruficervix*, *roraimae*, *decussatus* and *atripunctatus*, which may be largely sedentary. Race *bifasciatus* partly migratory, S birds moving N after breeding season to winter in chaco of N Argentina. Race *patagonicus* also partly migratory, S birds moving N and wintering in NE Argentina (Buenos Aires N to Formosa).

Status and Conservation. Not globally threatened. Uncommon migrant in parts of range, common breeding bird in many others. In Colombia, widespread and quite common; in Paraguay, apparently a fairly common winter visitor locally, though not recorded before 1979, possibly due to lack of coverage rather than a change in range; uncommon in Atlantic forest region, Brazil; widespread and probably not uncommon throughout much of Argentina and Chile.

Bibliography. Araya & Chester (1993), Belton (1984), Butler (1979), Canevari *et al.* (1991), Chapman (1931), Contreras & González (1991), Contreras *et al.* (1990), Davis *et al.* (1994), Fjeldså & Krabbe (1990), Fjeldså & Mayer (1996), Gilliard (1941), Hayes (1995), Hayes *et al.* (1994), Herzog *et al.* (1997), Hilty & Brown (1986), Johnson (1967), Kiff *et al.* (1989), Klimaitis & Moschione (1987), Koepcke (1970), Marín *et al.* (1989), Mayr & Phelps (1967), Meyer de Schauensee & Phelps (1978), Narosky & Yaurieta (1993), Nellar (1993), Parker & Goerck (1997), Parker *et al.* (1982), de la Peña (1994), Remsen & Traylor (1989), do Rosário (1996), Schubart *et al.* (1965), Sick (1979, 1993, 1997), Storer (1989), Stotz *et al.* (1996), Straube (1990), Todd & Carriker (1922), Wetmore (1926), Willard *et al.* (1991), Willis & Oniki (1993), Zimmer (1930).

38. White-tailed Nightjar

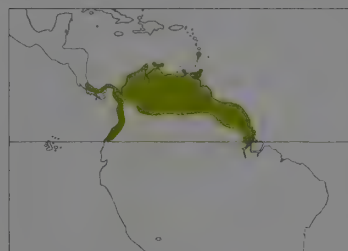
Caprimulgus cayennensis

French: Engoulevent coré **Spanish:** Chotacabras Coliblanco
German: Weißschwanz-Nachtschwalbe
Other common names: Cayenne Nightjar(!)

Taxonomy. *Caprimulgus cayennensis* J. F. Gmelin, 1789, Cayenne. Has been considered to have close affinities with *C. candicans*, forming superspecies or possibly even conspecific, but available evidence suggests that they may not be closely related. Species formerly listed as *C. albicauda*. Six subspecies recognized.

Subspecies and Distribution.

C. c. albicauda (Lawrence, 1875) - SE Costa Rica E to NW Colombia.
C. c. apertus J. L. Peters, 1940 - W Colombia S to extreme N Ecuador.
C. c. insularis (Richmond, 1902) - extreme NE Colombia, NW Venezuela, Margarita I and islands of Curaçao, Aruba and Bonaire.
C. c. manati (Pinchon, 1963) - Martinique.
C. c. leopetes Jardine & Selby, 1830 - Trinidad, Tobago, Bocas Is and Little Tobago.
C. c. cayennensis J. F. Gmelin, 1789 - EC & NE Colombia E through Venezuela, the Guianas and probably extreme N Brazil.



Descriptive notes. 20-22.5 cm; male 30-40 g, female 25-46 g. Sexually dimorphic. Upperparts greyish-brown, streaked blackish-brown; broad tawny-buff nuchal collar; wing-coverts greyish-brown, heavily spotted white, buff and pale buff; supercilium buffish or white, often indistinct; submoustachial stripe buffish or white. Male has thin whitish line across forewing, large white throat patch, buffish breast heavily spotted white, and white belly; female has buffish throat patch and is generally darker and buffier on underparts. Male shows a white band across four outermost primaries and a largely white tail; female lacks

white on wings and tail. Iris dark brown, bill blackish, legs and feet blackish-brown. Has more distinct nuchal collar than *C. parvulus*; supercilium more strongly marked, and tail more rounded; male shows paler underparts. Differs from *C. maculicaudus* in narrower, less pronounced supercilium and paler crown; also in white markings on wings. Immature plumages not described. Races generally vary in size, colour of nuchal collar and overall coloration; considerable colour variation even within nominate race. **VOICE.** Advertising call of male is a series of short, high-pitched whistles: "pt-cheeeeeee". Singing from low perches, mainly at dusk and dawn. Flight calls are high-pitched "see-see" notes; other calls include soft "tic-tic" or "wut-wut-wut".

Habitat. Typically open grassland and savanna with scattered vegetation, scrubland and along forest edges; also grassy hillsides with scattered bushes, pastures and large clearings such as airstrips. Occurs from sea-level up to possibly 3200 m.

Food and Feeding. Feeds on moths, beetles, bugs, damselflies, crickets and grasshoppers. Forages by making short sallies from ground, or by hunting low over vegetation and among animals.

Breeding. Breeds Feb-Jun in Costa Rica, Mar-Jul in Colombia, possibly Apr-Jun in Venezuela, Feb-Dec in Surinam, Jan-Jun on Trinidad, Feb-Jun on Tobago, and late Jan to Jul on Martinique. Nest-site recorded in rough grass and on gravel with nearby vegetation on Trinidad, on sparsely vegetated sandy ground in Surinam, on bare, stony ground near trees or in open savanna on Martinique; no nest, eggs laid on ground. Clutch 1-2 eggs, elliptical, pinkish-buff or creamy, scrawled, blotched or spotted lilac, grey and reddish-brown, markings denser around blunt end; incubation by female during day; chick semi-precocial; adults flushed from chicks perform injury-feigning distraction display.

Movements. Largely sedentary, although has occurred as a vagrant on Puerto Rico.

Status and Conservation. Not globally threatened. Fairly common throughout much of range, though local and uncommon in Panama, and scarce on Aruba, Curaçao and Bonaire (Netherlands Antilles). In Costa Rica, locally widespread on Pacific slope from Guanacaste southwards but status unclear on Caribbean slope; fairly common and widespread in Trinidad and Tobago, also occurring on Bocas Is and Little Tobago; probably not uncommon on Martinique, especially in E coastal plains, Caribbean lowlands and Lamentin plain along Gagneron embankment. Fairly common in Colombia, especially in grasslands; rather common in Surinam, especially in open, sandy savannas; widely distributed and not uncommon in Guyana; possibly not particularly common in Ecuador, where first recorded in Imbabura province Oct 1983.

Bibliography. Benito-Espinal & Hautecastel (1988), Bond (1985), Chapman (1931), French (1991), Friedmann & Smith (1950), Gilliard (1941), Haverschmidt & Mees (1994), Herklots (1961), Hilty & Brown (1986), Meyer de Schauensee & Phelps (1978), Pinchon (1963, 1976), Raffaele *et al.* (1998), Ridgely & Gwynne (1989), Schmitt & Schmitt (1990), Sick (1993, 1997), Slud (1964), Snyder (1966), Stiles & Skutch (1989), Stotz *et al.* (1996), Tostain *et al.* (1992), Voous (1965, 1983), Wetmore (1968a).

39. White-winged Nightjar

Caprimulgus candicans

French: Engoulevent à ailes blanches **Spanish:** Chotacabras Aliblanco
German: Weißflügel-Nachtschwalbe

Taxonomy. *Stenopsis candicans* Pelzelin, 1867, Irsanga, São Paulo, Brazil. Has been considered to have close affinities with *C. cayennensis*, forming superspecies or possibly even conspecific, but available evidence suggests that they may not be closely related; current treatment requires further study, as present species may actually belong in genus *Eleothreptus*. Monotypic.

Distribution. N Bolivia, SC Brazil and E Paraguay.



Descriptive notes. 19-21 cm; male 46-51 g. Sexually dimorphic. Upperparts and inner wing-coverts pale greyish-brown, speckled, barred and streaked brown; boldly spotted blackish on crown, no nuchal collar; outer wing-coverts white, edged brown and boldly spotted blackish; scapulars greyish-brown boldly marked blackish, inner webs generally buffish; broad pale buff submoustachial stripe; row of buffish spots around lower throat; breast greyish-brown tinged chestnut and tawny, barred and speckled brown; rest of underparts white. In flight, male has whitish wings and a largely white tail; female lacks white in plumage, has scapulars more boldly marked blackish and has buffish underparts. Iris reddish-brown or chestnut, bill generally blackish with flesh-coloured base, legs and feet grey or greyish-flesh. Immature only very recently described: similar to adult but slightly browner and less greyish, with no

white on wings and tail. **Voice.** Territorial calls of male are short, undulating whistles, "tshere-she-shew"; alarm calls include similar whistles and abrupt "eek" calls.

Habitat. Typically open grasslands with scattered trees and bushes: Chaco woodland, dry open savannas, and open *cerrado* or grassland with scattered bushes, palms, termite mounds and anthills. Also in grasslands regenerating after fires. Avoids areas of tall grass. A lowland species, recorded from sea-level to 210 m.

Food and Feeding. Known to feed on beetles and moths. Forages over hillsides, hilltops and *cerrado*, including burnt areas.

Breeding. Until recently, almost unknown. Single nest known to date was found in E Paraguay, Nov 1997, in *campo sucio* grassland with *Butia paraguayensis* palms: no nest as such, with eggs laid on bare earth: site was open from above, eggs partially covered by a herb. Clutch 2 eggs, pale creamy-brown lightly covered with darker brown, and speckled greyer. Female was incubating in mid-late Nov; 1 juvenile fledged by mid-Jan.

Movements. Largely unknown, although may be migratory in parts of range.

Status and Conservation. CRITICALLY ENDANGERED. Until fairly recently, known only from two museum specimens dating from 1820's. Considered not uncommon at Das Emas National Park, Goiás, in Brazil in 1980's, and legally protected in that country. Possibly fairly common at Aguara Nu in Reserva Natural del Bosque Mbaracayú, E Paraguay, where up to 20 pairs discovered in suitable habitat Sept-Dec 1995; continued work in Jul-Nov 1997, involving marking and radio-tracking birds, gave estimated population of 30-50 birds. Male captured at Beni Biological Station in N Bolivia in Sept 1987 suggests possibility of a population in this area, though not recorded there again as yet. Seriously threatened by loss of breeding habitat to agriculture and ranching, and to grass fires, often started deliberately.

Bibliography. Anon. (1995d), Brace *et al.* (1997), Clay, Capper *et al.* (1998), Clay, Esquivel & Mazar (1999), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Davis & Flores (1994), Hayes (1995), López *et al.* (1998), Lowen, Bartrina, Brooks *et al.* (1996), Lowen, Bartrina, Clay & Tobias (1996), Lowen, Clay *et al.* (1997), Redford (1987), Ruschi (1979), Short (1975), Sick (1993, 1997), Stotz *et al.* (1996), Tobias & Lowen (1996), Wege & Long (1995), Willis (1992).

40. Spot-tailed Nightjar

Caprimulgus maculicaudus

French: Engoulevent à queue étoilée

Spanish: Chotacabras Colipinto

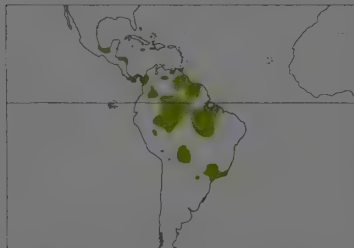
German: Fleckschwanz-Nachtschwalbe

Other common names: Pitsweet

Taxonomy. *Stenopis maculicaudus* Lawrence, 1862, Pará, Brazil.

Considered by some authors sufficiently distinctive to merit isolation in a separate genus, in which case *Antius* is available. Disjunct populations could represent more than one species. Monotypic.

Distribution. Discontinuously from SE Mexico to the Guianas; and discontinuously from NW & N Brazil S through SE Peru, N & EC Bolivia to E Paraguay and SE Brazil.



Descriptive notes. 19-21.5 cm; male 28-35 g, female 26-39 g. Sexually dimorphic. Crown blackish-brown spotted buff or tawny; upperparts brown or greyish-brown, barred and vermiculated dark brown, buff and tawny; distinct buff or tawny nuchal collar; wing-coverts brown heavily speckled pale buff and boldly spotted buff or cinnamon, with broad buffish line along scapulars; broad buff supercilium, thin buff submoustachial stripe, triangular blackish malar stripe and small buff or cinnamon-buff throat patch; breast brownish, spotted buff, cinnamon-buff or buffish-white; distinct cinnamon rufous band, thinly barred brown, on lower breast and upper belly; rest of underparts buff indistinctly barred brown.

Both sexes lack white markings on wings, but may show thin buff trailing edge to inner wing. Male has broad white tips to all but central pair of tail feathers, and white spot along inner webs of four outermost tail feathers (noticeable only on fanned tail); female has no white in tail. Iris brown, bill blackish, legs and feet greyish. Differs from *C. cayennensis* in darker crown and more pronounced supercilium; male lacks white wing band of that species and has less white in tail, while both sexes show buffish trailing edge to inner wing. Differs from *C. parvulus* by more distinct nuchal collar, and throat patch less distinct and cinnamon-buff, not white; supercilium much more distinct; also male lacks white wing spots of that species, and both sexes have buffish trailing edge to inner wing. Immature similar to adult. **Voice.** Song of male is a repetitive, high-pitched "t-seet", song notes variable, given from ground or low perches, mainly at dusk. Calls include rapidly repeated "t-seet", accelerating "t-seet, seet-seet" and shrill "seeu" or "see-ee-eei" notes.

Habitat. Mainly savanna and grassland with scattered trees and thickets; also bushy pastures, open marshy country, clearings, second growth, and woodland edges. In Brazil also found in burnt groves, in Honduras and NE Nicaragua recorded in pine savanna, and in Venezuela possibly frequents rainforest. Recent records from Paraguay come from marshy valley and nearby drier hill slopes adjacent to gallery forest. Reported from sea-level to 500 m.

Food and Feeding. Feeds on beetles, moths, flies, bugs, Orthoptera and damselflies. Forages by making flycatching sallies from ground.

Breeding. Breeds late Mar to Jul in Mexico, Oct-Jan in Surinam, and possibly late Feb to May in Colombia; data from other regions unavailable. No nest, eggs laid on ground, often in open, grassy area close to low bushes. Clutch 2 eggs, buff or creamy-pink, spotted or flecked reddish-brown and pale lilac, markings heavier at blunt end; chick semi-preocial, covered in blackish down with brownish-buff markings; adults flushed from chicks may perform distraction display.

Movements. Sedentary throughout much of South American range, though small population migratory, occurring as breeding summer visitor to parts of Central America, e.g. SE Mexico (late Mar to Aug). Recorded in C Honduras (L. Yojoa) as migrant only.

Status and Conservation. Not globally threatened. Fairly common locally in many parts of range, though probably under-recorded in many regions. Locally common to fairly common in SE Mexico, though possibly breeding visitor only, wintering areas remaining unknown; possibly not common in Colombia; widespread but local in Brazil, especially in S; recently reported from E Paraguay, where 2 birds noted in Reserva Natural del Bosque Mbaracayú, Sept 1995.

Bibliography. Binford (1989), Blake (1949), Dubs (1992), Forrester (1993), Haffer (1975), Haverschmidt & Mees (1994), Hilty & Brown (1986), Howell & Webb (1995a), Kirwan & Sharpe (1999), Lowen, Bartrina, Brooks *et al.* (1996), Lowen, Clay *et al.* (1997), Meyer de Schauensee & Phelps (1978), Monroe (1968), Parker *et al.* (1982), Rensen & Traylor (1989), Ridgely & Gwynne (1989), Schubart *et al.* (1965), Sick (1993, 1997), Snyder

(1966), Stotz *et al.* (1996), Tostain (1980), Tostain *et al.* (1992), de Urioste (1994), Willis (1992), Willis & Oniki (1993), Zimmerman (1957b).

41. Little Nightjar

Caprimulgus parvulus

French: Engoulevent des bois

German: Zwernachtschwalbe

Spanish: Chotacabras Chico

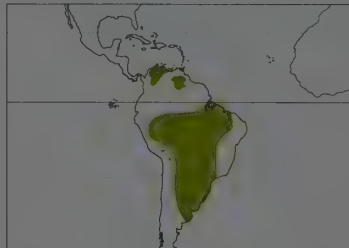
Taxonomy. *Caprimulgus parvulus* Gould, 1837, near Santa Fé, River Paraná, Argentina.

Formerly considered conspecific with *C. anthonyi*, but differs in vocalizations. Birds of Santa Marta region (N Colombia) have been considered a separate species, *C. heterurus*, again on basis of vocal differences, but these are normally considered insufficiently marked to justify such a split. Two subspecies currently recognized.

Subspecies and Distribution.

C. p. heterurus (Todd, 1915) - N Colombia and NW & CE Venezuela.

C. p. parvulus Gould, 1837 - E Peru through Brazil (S of Amazon) and S to N Argentina and Uruguay.



Descriptive notes. 19-21 cm; male 25-42 g, female 36-46 g. Sexually dimorphic. Upperparts greyish-brown streaked blackish-brown, broadly so on crown; broad but indistinct buff or tawny-buff nuchal collar; wing-coverts greyish-brown, barred, spotted and speckled buff, tawny, rufous and whitish; scapulars blackish-brown, broadly edged buff or pale buff on outer webs; no supercilium but large white throat patch; underparts greyish-brown spotted pale buff and greyish-white, thinly barred light brown, becoming buff barred brown on belly and flanks. Male has large white spot on four outermost primaries and

white tips to all but central pair of tail feathers; female generally lacks white. Iris dark brown, bill blackish, legs and feet brownish-olive or greyish-olive. Differs from *C. maculicaudus* by less marked nuchal collar, much fainter supercilium, and large white throat patch; male also by white markings in wings; from *C. cayennensis* by somewhat less distinct nuchal collar and supercilium, and by squarer tail; and from *C. anthonyi* by plainer scapular pattern and smaller white throat patch. Immature similar to adult female. Race *heterurus* similar, but slightly darker on underparts and commonly has larger white markings on wings and tail; overall tone of coloration apparently variable in both races, but generally fairly grey. **Voice.** Song of male is a distinctive, warbled "dop, dro-dro-dro-dro", descending in pitch; sings from perches throughout night. Song of race *heterurus* is a deeper, evenly pitched "pik, gobble-gobble-gobble-gobble".

Habitat. Varied, including open woodland and forest, lightly wooded terrain, savanna, thickets, open bush country, pastures and weedy fields with scattered bushes, and espinillo or eucalyptus groves. In Venezuela, race *heterurus* often found in slightly hilly terrain and also recorded in suburban parkland. Occurs from sea-level to 1000 m.

Food and Feeding. Feeds on moths and beetles. Foraging methods not described.

Breeding. Poorly documented. Possibly breeds from late Oct in Colombia, Oct-Nov in Paraguay, and from Nov in SW Brazil. No nest, eggs laid on ground, often near or beneath thick bush. Clutch 2 eggs, elliptical, creamy-white to buffish-white, blotched and scrawled brown, with underlying patches of lavender-grey; chick not described.

Movements. Nominate race possibly sedentary and partly migratory, though movements poorly understood. As a migrant, occurs from E Peru E to N Brazil (Pará). In E Brazil (Minas Gerais) often very common in Oct, and summer visitor only to S Brazil (late Oct to mid-Feb). Race *heterurus* probably sedentary.

Status and Conservation. Not globally threatened. Published data on status rather scarce, but in many regions often common to abundant in suitable habitat. Rare in N Colombia, though possibly under-recorded; in Brazil, common Apr-Oct in Mato Grosso, and locally common summer visitor, late Oct to mid-Feb, in W & C Rio Grande do Sul; generally rare to uncommon in much of Paraguay, though common in Alto Chaco in W; possibly not uncommon locally in N Bolivia.

Bibliography. dos Anjos *et al.* (1997), Bauer *et al.* (1997), Belton (1984), Brace & Hornbuckle (1998), Canevari *et al.* (1991), Chubb (1910), Contreras *et al.* (1990), Davis, L.L. (1979a), Davis, S.E. (1993), Donahue (1994), Dubs (1992), Hayes (1995), Hilty & Brown (1986), Meyer de Schauensee & Phelps (1978), Miserendino (1998), Narosky & Yzurieta (1993), Nellar (1993), Parker *et al.* (1982), de la Peña (1994), Rensen & Traylor (1989), do Rosário (1996), Saibene *et al.* (1996), Schubart *et al.* (1965), Schwartz (1968), Short (1975), Sick (1993, 1997), Stotz *et al.* (1996), Wetmore (1926).

42. Scrub Nightjar

Caprimulgus anthonyi

French: Engoulevent d'Anthony

Spanish: Chotacabras de Anthony

German: Equadornachtschwalbe

Taxonomy. *Setopagis anthonyi* Chapman, 1923, Portovelo, Ecuador.

Formerly considered conspecific with *C. parvulus*, but differs in vocalizations. Monotypic.

Distribution. W Ecuador and NW Peru.



Descriptive notes. 18-21 cm; male 32-39 g, female 31-42 g. Sexually dimorphic. Upperparts greyish-brown, speckled buffish and streaked blackish-brown; crown broadly streaked blackish-brown; indistinct tawny-buff nuchal collar; wing-coverts greyish-brown, speckled brown and buffish and heavily spotted buff and pale buff; scapulars blackish-brown, broadly edged buff; white throat patch; underparts greyish-brown or brown, broadly barred buff and pale buff. Male has white band across five outermost primaries and white inner webs to two outermost tail feathers; female has thinner white wing bands and less white on tail. Iris dark brown,

bill blackish, legs and feet pinkish grey-brown. Differs from *C. parvulus* in different scapular pattern and smaller white throat patch; from *C. cayennensis* by less distinct tawny-buff nuchal collar. Imma-

ture similar to adult but generally lacks white markings on wings and tail. Voice. Advertising song of male is a short, repetitive whistle, "wheeeeo" or "t-wheeeeo", given from ground and low perches, mainly at dusk and dawn. Flight call is a soft "tuk, tuk, tuk"; also gives a rolling "quaqrrr", usually from a perch.

Habitat. Prefers arid scrubland with scattered trees and bushes, dry open grassland and edges of deciduous woodland. Also near roads through dry deciduous forest, and in brushy mesquite woodland, thickets of second-growth mesquite, fallow farmland, wet pastures and damp grassy meadows. Recorded from sea-level to 775 m.

Food and Feeding. Feeds on moths, grasshoppers and beetles. Forages low over vegetation.

Breeding. Poorly known. Breeding commences at start of rains, which often highly irregular; season possibly Dec-Mar. Possibly double-brooded during prolonged rains, but may not breed at all in dry years. Nest-site often in small clearing in fairly dense vegetation, along edge of thicket or beneath tree; no nest, eggs laid on leaf litter on ground. Clutch 1-2 eggs, elliptical, pinkish-buff, heavily speckled and scrawled brown, reddish-brown and grey; chick not described.

Movements. Poorly understood. May be partially nomadic, moving seasonally with rains. No other information available.

Status and Conservation. Not globally threatened. Restricted-range species: present in Tumbesian Region EBA and Marañón Valley EBA. Range restricted to arid, coastal lowlands of W Ecuador and lowlands and hills at foot of W slope of Andes in NW Peru. In Ecuador, apparently locally common in suitable habitat, e.g. common and widespread on Santa Elena Peninsula; possibly increasing in some areas as a result of deforestation; present in Machalilla National Park (W Ecuador).

Bibliography. Best & Kessler (1995), Best *et al.* (1996), Chapman (1923), Meyer de Schauensee (1982), Parker, Parker & Plenge (1982), Parker, Schulenberg *et al.* (1995), Robbins *et al.* (1994), Schwartz (1968), Stattersfield *et al.* (1998), Stotz *et al.* (1996).

43. Cayenne Nightjar *Caprimulgus maculosus*

French: Engoulevent de Guyane

Spanish: Chotacabras Guayanés

German: Cayennenachtschwalbe

Taxonomy. *Nyctipolus maculosus* Todd, 1920, Tamanor, French Guiana. Monotypic.

Distribution. French Guiana.



Descriptive notes. 22.5 cm. Known only from type specimen, a male. Upperparts greyish-brown, broadly streaked blackish-brown on crown and nape; narrow, indistinct tawny nuchal collar; wing-coverts greyish-brown heavily spotted buff; scapulars blackish-brown, broadly edged buff; large white patch on either side of lower throat; underparts buff, heavily barred brown. Small white spot on four outermost primaries and broad white tips to three outermost tail feathers. Iris possibly dark brown, bill blackish, legs and feet dark brown. Paler, less black than *C. nigrescens*, with different pattern on scapulars. Immature plumages

not described. Voice. Unknown.

Habitat. Probably a forest species, inhabiting clearings, open areas and riversides; type specimen was taken in an area of such habitat, near lower reaches of a boulder-strewn river.

Food and Feeding. Presumably feeds on insects, but neither food nor foraging methods known.

Breeding. No information.

Movements. Unknown.

Status and Conservation. Not globally threatened. Data-deficient. Almost certainly merits treatment as a restricted-range species. True status unclear, but available evidence suggests species unlikely to be common, and might well be threatened. Known only from type specimen, taken Apr 1917 at Saut Tamanor on Fleuve Mana, c. 10 km above its confluence with R Cockioco, in French Guiana. Identity of a possible female caught at Saül airstrip, also in French Guiana, in Sept 1982 remains unconfirmed.

Bibliography. Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Ingels (1988), Meyer de Schauensee (1982), Olrog (1968), Stotz *et al.* (1996), Todd (1920), Tostain *et al.* (1992), Wege & Long (1995).

44. Blackish Nightjar *Caprimulgus nigrescens*

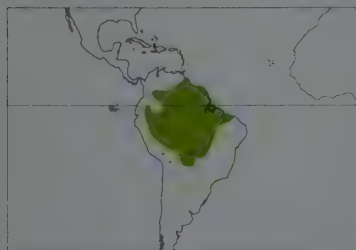
French: Engoulevent noirâtre

German: Trauernachtschwalbe

Spanish: Chotacabras Negruzco

Taxonomy. *Caprimulgus nigrescens* Cabanis, 1848, lower Essequibo River, Guyana. Forms superspecies with *C. whitelyi*. Monotypic.

Distribution. E Colombia and E Ecuador E through the Guianas and N Brazil, S to N & E Bolivia.



Descriptive notes. 19.5-21.5 cm; male 32-42 g, female 32-50 g. Sexually dimorphic. Upperparts blackish, heavily mottled tawny, cinnamon, buff and greyish-white, no nuchal collar; wing-coverts blackish, speckled and spotted buff, tawny, cinnamon and greyish-white; scapulars blackish-brown spotted tawny, often edged buff; small white patch on either side of lower throat; underparts dark brown, barred and spotted buff, buffish-white, tawny and cinnamon, becoming buffish barred brown on lower belly and flanks. Male has small white spot on second, third and fourth outermost primaries, and white tips to second

and third outermost tail feathers, occasionally also on inner web of outermost and outer web of fourth outermost; female lacks white markings on wings and tail. Iris dark brown, bill blackish, legs and feet dark brown. Slightly smaller than *C. whitelyi*, which occurs at higher altitudes in Pantepui of E Venezuela; present species has smaller white throat patch and bold white spots on tertials and inner wing-coverts, and more marked scapular pattern. Smaller and darker than *C. longirostris*, and lacks the broad tawny nuchal collar; different wing and tail markings. Immature

similar to adult but often slightly paler. Voice. Song of male is a soft, purring "pru.r.r.r." or "qu.r.r.r.t", given from rocks or other perches throughout night. Alarm calls are short, sharp "pink" or "prek" notes; gives guttural hissing sounds during threat, defence and distraction displays.

Habitat. Mainly sparsely vegetated, open stony country with granite outcrops, and rocky places in and along rivers; also rainforest, second growth, and open savanna with scattered bushes. Away from rocks, frequently found near tracks, in clearings and on recently burnt ground. Recorded from 100 m to 1100 m.

Food and Feeding. Feeds on moths, beetles and other insects. Forages over rocky outcrops and above tree canopy.

Breeding. Breeds possibly May-Aug in Guyana, Feb-Mar and Aug-Nov in Surinam (coinciding with dry season, though eggs found in all months except May and Dec), Sept-Oct in Bolivia, and Aug-Nov in W Brazil; no data from other regions. Normally double-brooded. Nest-site often close to vegetation in clearing or burnt area, alongside forest road, track or river, on granite outcrop or on exposed rock on river island; no nest, egg laid on bare ground, sandy soil or leaf litter, or in shallow depression up to 20-30 mm deep on granite rock. Clutch 1 egg, elliptical, slightly glossy, creamy-buff, pinkish-buff or reddish-brown, spotted and blotched brown and grey; replacement may be laid if clutch unsuccessful; incubation by both adults, period possibly c. 17 days; adults threatened at nest-site perform injury-feigning distraction display on ground; chick semi-precocial, covered in pale greyish down, fledges after c. 14 days and leaves nesting area within 16-18 days.

Movements. None recorded. Sedentary.

Status and Conservation. Not globally threatened. Abundant in suitable habitat throughout Amazon basin. Very common in some regions of Colombia such as Guainía and Vaupés, especially in areas of savanna woodland interspersed with cerros and rocky outcrops; widely distributed and common in Surinam and Guyana. Present in several protected areas, e.g. Amacayacu National Park (Colombia), Imataca Forest Reserve (Venezuela) and Voltzberg-Raleigh Falls Reserve (Surinam). Eggs and young often at risk from extreme temperatures or precipitation, especially those at nest-sites on granite surfaces, and potential predators include various mammals, birds and reptiles.

Bibliography. Blake (1950b), Friedmann (1948), Gilliard (1941), Haverschmidt & Mees (1994), Hilty & Brown (1986), Ingels (1988), Ingels & Ribot (1982, 1983), Ingels *et al.* (1984), Meyer de Schauensee & Phelps (1978), Parker *et al.* (1982), Remsen & Traylor (1989), Roth (1985), Sargeant (1994), Schubart *et al.* (1965), Sick (1993, 1997), Snyder (1966), Stotz *et al.* (1996), Tostain *et al.* (1992), Willard *et al.* (1991).

45. Roraiman Nightjar *Caprimulgus whitelyi*

French: Engoulevent du Roraima

Spanish: Chotacabras del Roraima

German: Roraimanachtschwalbe

Taxonomy. *Antrostomus whitelyi* Salvin, 1885, Mt Roraima, Venezuela.

Forms superspecies with *C. nigrescens*. Monotypic.

Distribution. Pantepui of SE Venezuela, and possibly also adjacent areas of Guyana and N Brazil. Known only from Cerros Roraima, Ptari-tepui, Jaua, Urutaní and Duida.



Descriptive notes. 21 cm; male 30-40 g, female 45-48 g. Sexually dimorphic. Upperparts blackish, spotted cinnamon, buff, greyish-white and tawny, no nuchal collar; wing-coverts blackish, spotted cinnamon, tawny and buff, no obvious scapular pattern; fairly large white patch on throat, rest of underparts dark brown, barred buff or buffish-white, becoming buff barred brown on belly. Male has thin white bar on three outermost primaries and large white spot on tips of inner webs of second and third outermost tail feathers; female has thin tawny bars on outer primaries and smaller white tail spots. Iris dark brown, bill blackish, legs and

feet dark brown. Slightly larger than *C. nigrescens*, with larger white throat patch, and white spots on tertials and inner wing-coverts; male of present species also differs in having white bars, not spots, on outer primaries and white tips only across inner webs of second and third outermost tail feathers. Smaller and generally darker than *C. longirostris* without the broad tawny nuchal collar of that species, and with different wing and tail markings. Immature plumages not described. Voice. Unknown.

Habitat. Apparently confined to humid, forested slopes and summits of tepuis (tabletop mountains), typically in open areas and clearings with scattered, dense vegetation. Recorded between 1280 m and 1800 m.

Food and Feeding. Probably feeds on insects. Foraging methods not described.

Breeding. No information.

Movements. None recorded. Sedentary.

Status and Conservation. Not globally threatened. Restricted-range species: present in Tepuis EBA. Currently considered Near-threatened. Probably not very common within its restricted and remote range, but poorly known.

Bibliography. Chapman (1931), Dickerman & Phelps (1982), Ingels (1988), Mayr & Phelps (1967), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Olrog (1968), Phelps (1938), Sick (1993, 1997), Stattersfield *et al.* (1998), Stotz *et al.* (1996).

46. Pygmy Nightjar *Caprimulgus hirundinaceus*

French: Engoulevent pygmée

German: Spixnachtschwalbe

Spanish: Chotacabras Pigmeo

Taxonomy. *Caprimulgus hirundinaceus* Spix, 1825, River Solimões; error = Feira de Sant'Anna, Bahia, Brazil.

Three subspecies recognized.

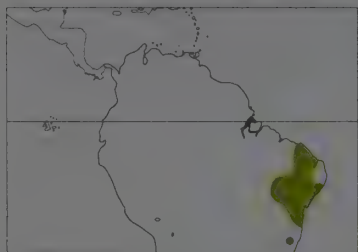
Subspecies and Distribution.

C. h. cearae (Cory, 1917) - NE Brazil (N Ceará to extreme N Bahia).

C. h. hirundinaceus Spix, 1825 - NE Brazil (S Piauí to Bahia and Alagoas).

C. h. vielliardi Ribon, 1995 - E Brazil (Colatina, Espírito Santo).

Descriptive notes. 16-20 cm. Sexually dimorphic. Upperparts and wing-coverts greyish-brown, densely speckled greyish-white or tawny and buff; no scapular pattern and no nuchal collar or an indistinct buff collar; thin whitish supercilium and indistinct buff submoustachial stripe; large white patch on throat with broad cinnamon-buff band below; underparts brown, densely spotted and barred



female lacking white on wings and generally also on tail. *Chordeiles pusillus* is usually browner and more variable in colour with a smaller white throat patch and whiter underparts; male has more defined white wing band, buffish-white trailing edge to inner wing and white tips to inner webs of second, third and fourth outer tail feathers; female has thinner white wing bands, duller trailing edge to inner wing and smaller white tips to tail feathers. Immature of present species paler than

pale buff and greyish-white, becoming buff barred brown on belly and flanks. Male has white spot on four outermost primaries and white tips to two outermost tail feathers (inner web only on outermost); female has smaller wing spots and lacks white on tail. Iris dark brown, bill blackish-brown, legs and feet blackish-brown. Somewhat similar to *C. parvulus*, which is browner and more variegated with blackish-brown scapulars broadly edged buff, broad but indistinct nuchal collar, no supercilium and a large white throat patch; male has larger white wing spots and white tips to all but central pair of tail feathers,

adult, often with strong cinnamon wash; primaries with broad buff tips. Races vary clinally in coloration: *cearae* paler, with less barring on underparts, which are sometimes plain, and larger white wing spots in male; *vielliardi* darker, with longer wings, and smaller white wing spots in male. VOICE. Song of male is a short, whistled "wheeo" or "wheo", often preceded by 3-4 rapid "wha" notes. Flight calls also "wha, wha, wha" notes.

Habitat. Typically woodland, but also cleared areas; newly described race *vielliardi* inhabits rocky areas.

Food and Feeding. Probably feeds on insects. Forages in open country but methods not described. **Breeding.** Poorly documented. Nest-sites recorded beside dirt roads and tracks.

Movements. None documented. All races possibly sedentary.

Status and Conservation. Not globally threatened. Restricted-range species: present in North-east Brazilian Caatinga EBA. Currently considered Near-threatened. Previously considered endemic to caatinga of NE Brazil but a disjunct population in Colatina, Espírito Santo, first recorded in 1980's, has now been described, suggesting further populations may possibly await discovery. Few data available from most of range, but not rare in Capiwara National Park, SE Piauí; also present in Parque Estadual da Pedra Talhada, 160 km W of Maceió, in Alagoas.

Bibliography. Cory (1917), Ferreira & Cunha (1996), Hellmayr (1929), Meyer de Schauensee (1982), Olmos (1993), Olrog (1968), Ribon (1995), Ruschi (1979), Sargeant (1996), Sick (1993, 1997), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Whitney (1996), Willis (1992).

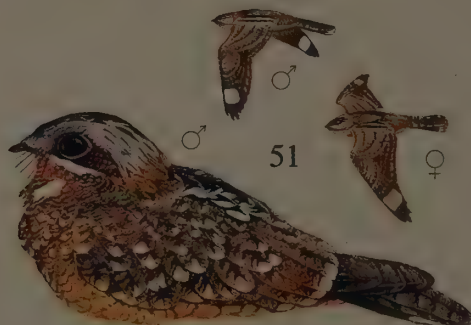
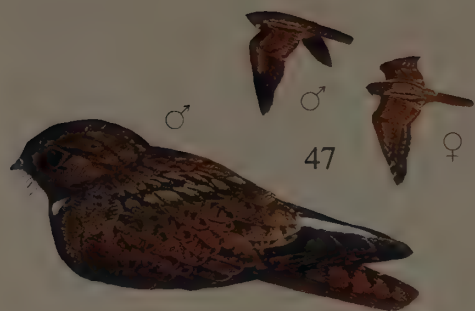
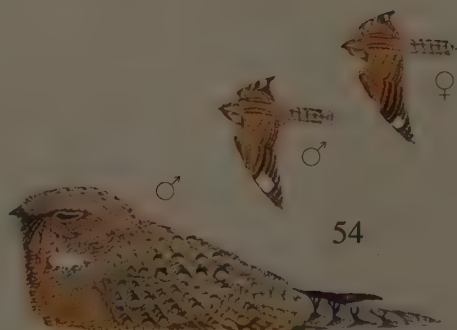


PLATE 31

inches 5
cm 13



47. Brown Nightjar *Caprimulgus binotatus*

French: Engoulevent à deux taches **Spanish:** Chotacabras Bimaculado
German: Bootschwanz-Nachtschwalbe
Other common names: Dusky Nightjar(!)

Taxonomy. *Caprimulgus binotatus* Bonaparte, 1850. Borneo; error = Ashanti, Dabocrom, Ghana. Current treatment requires further study; formerly split off in monotypic genus *Veles*, and notable morphological peculiarities suggest that this may indeed be appropriate (see page 306). Monotypic.
Distribution. Liberia discontinuously E to C Zaire, where restricted to rainforest zone.



Descriptive notes. 21–23 cm; 1 unsexed 63 g. Sexes similar, but female somewhat paler above. Upperparts and wing-coverts dark brown, densely mottled and flecked tawny and chestnut-brown, no nuchal collar; small white spot on either side of lower throat; rictal bristles short and weak; underparts dark brown, mottled and barred tawny and chestnut-brown; outer primaries curved, tail stiff and held in inverted V when bird at rest; both sexes lack white markings on wings and tail. Iris brown, bill blackish, legs and feet dark brown. Immature similar to adult, but scapulars and inner coverts pale greyish-buff, spotted dark brown.

VOICE. Song of male is a repetitive series of “twoh” or “kliou” notes, given from perches or in flight.
Habitat. Mainly lowland primary rainforest, often with open canopy and thick understorey. Found in semi-evergreen or semi-deciduous forest. In SW Central African Republic, also recorded at edges of *Raphia* swamps in dense rainforest.

Food and Feeding. Feeds on insects. Forages by making flycatching sallies from perches, usually hawking close to forest canopy.

Breeding. Poorly known. Possibly breeds Jan-Mar in Liberia, Feb-Mar in Central African Republic, and May-Jun in Cameroon. Possibly territorial. Nest-site possibly above ground, e.g. on arched leaves of *Raphia* palms.

Movements. None recorded. Sedentary.

Status and Conservation. Not globally threatened. Possibly eligible for listing as threatened species. Probably uncommon to rare throughout range and generally confined to lowland rainforest; possibly under-recorded. Rare in Ghana, though some habitat protected, e.g. a few records since 1970's from Ahanta Forest Reserve; local and rare in Cameroon, though present in protected areas such as Korup National Park; possibly not uncommon locally in extreme N Congo, with 7 singing males located in Nouabalé-Ndoki National Park in 1997, territories 500–1000 m apart in suitable habitat; probably not common in Zaire. Loss of habitat through deforestation main potential threat.

Bibliography. Bannerman (1953), Brosset & Éard (1986), Carroll (1988), Carroll & Fry (1987), Christy & Clarke (1994), Colston & Curry-Lindahl (1986), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Dowsett-Lemaire & Dowsett (1998a, 1998b), Dutton & Branscombe (1990), Evans (1993), Fry (1988b), Fry *et al.* (1988), Gatter (1997), Grimes (1987), Lippens & Wille (1976), Louette (1981, 1990b, 1990c), Mackworth-Præd & Grant (1970), Rodewald *et al.* (1994), Snow (1978).

48. Red-necked Nightjar *Caprimulgus ruficollis*

French: Engoulevent à collier roux **Spanish:** Chotacabras Cuellirrojo
German: Rothals-Ziegenmelker

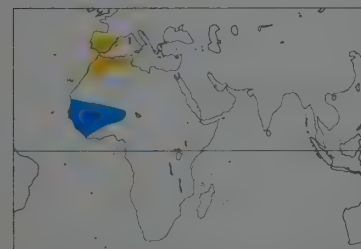
Taxonomy. *Caprimulgus ruficollis* Temminck, 1820. Algeciras, Spain. Two subspecies recognized.

Subspecies and Distribution.

C. r. ruficollis Temminck, 1820 - Spain, Portugal and N Morocco.

C. r. desertorum Erlanger, 1899 - NE Morocco, N Algeria (S to Great Atlas Mts) and N Tunisia.

Winters mainly in W Africa.



Descriptive notes. 30–32 cm; male 70–102 g, female 81–86 g, unsexed 60–119 g. Sexually dimorphic. Upperparts greyish-brown streaked blackish-brown; broad buff or tawny-buff nuchal collar; wing-coverts greyish-brown boldly spotted buff; scapulars blackish-brown, broadly bordered buff on outer webs; prominent white or buffish-white submoustachial stripe and white throat patch; underparts greyish-brown, speckled greyish-white barred brown, becoming buff barred brown on belly and flanks. Male has large white spot on three outermost primaries (usually inner webs only) and broad white tips to two outermost tail feathers.

female has smaller wing and tail spots. Iris dark brown, bill blackish-brown, legs and feet greyish-brown. Larger and generally paler and less brown than *C. europæus*, which shows distinct buffish line across wing-coverts and white primary patch closer to wingtip. Immature similar to adult but paler, with buffish wing and tail markings. Race *desertorum* is paler, more sandy-buff, often tinged rufous, with narrower streaking on crown and broader nuchal collar. Voice. Song of male is a repetitive series of loud “cut-ok” notes, often preceded by rapid “quot” calls, chuckles or gurgles; sings from perches throughout night. Flight call is a single or double-noted “cutow”; incubating adult may give accelerating, knocking notes. All birds make guttural hissing sounds during threat/defence displays.

Habitat. Typically lowlands and hillsides, with scattered vegetation and bare ground, in pine woodland, coastal forest, eucalyptus or olive plantations, vineyards, open scrubland with cork oak (*Quercus suber*), prickly pear (*Opuntia*) or scattered trees, and dense thickets of broom, gorse, bramble, tree

heath (*Erica arborea*) or pistachio (*Pistacea lentiscus*). Also semi-deserts, and in Tunisia cactus plantations. Tends to avoid treeless country and sand dunes. Recorded from sea-level to 1500 m.
Food and Feeding. Diet includes moths, moth larvae, locusts and locust nymphs, mosquitoes, flies, grasshoppers, beetles and caterpillars. Also ingests items such as small seeds, earth and grains of sand, possibly by accident. Forages in open habitats, sometimes high up and usually alone. Occasionally forages on ground.

Breeding. Breeds early May to late Aug in Spain and Portugal, and mid-May to Aug in C Morocco, Algeria and Tunisia. Possibly double-brooded. Probably monogamous; territorial; usually solitary, but in Tunisia nests sometimes in loose groups 2–20 m apart. Nest-site in open, beneath or among low bushes, beside fallen log or branch or under tree, in Tunisia also in cactus plantation, in S Portugal also among coastal driftwood on sandbank; no nest, eggs laid on ground, usually on leaf litter or pine needles. Clutch usually 1–2 eggs, elliptical, glossy white or creamy-white, marbled and blotched grey and brown; incubation usually by female, at least during day, period generally 14–19 days, eggs hatching asynchronously; chick semi-precocial, covered in brownish-buff down; female threatened at nest-site may perform injury-feigning distraction display; chicks make first flights at c. 16–18 days and become independent after 4–5 weeks.

Movements. Migratory. Nominate race leaves breeding grounds by late Oct or Nov. Regular autumn migrant through Gibraltar, along coast of Morocco and across NW Africa (e.g. W & C Mauritania Oct–Nov). Some may winter in Morocco (e.g. Chichaoua Dec–Jan) but usually winters farther S in W Africa, though exact range unclear. Recorded N Senegal late Nov and Jan, and C & S Mali Oct–Mar, where common and widespread. In spring, return movements on broad front (Mar to early May) across Mauritania, Western Sahara, Morocco and W Algeria, returning to breeding grounds from late Apr to May. Race *desertorum* migratory and partially sedentary; movements and wintering range probably similar to nominate race. Recorded N Senegal late Nov, E Gambia Nov, and Mali, Ivory Coast and N Ghana (Gambaga) Mar. Winter records (race unknown) also from Liberia in Dec and Ivory Coast in Nov and Jan. Vagrants recorded in Britain, Denmark, Ibiza, Sicily, Malta, Libya and Madeira and possibly Yugoslavia, Turkey and Canary Is; single record from France during present century, a bird found dead at Bouches-du-Rhône in Jun 1997.

Status and Conservation. Not globally threatened. Reasonably common in Spain with 100,000–131,000 breeding pairs, range and population levels apparently not declining; locally common in Portugal with 1000–10,000 pairs, but declining in Algarve region due to habitat loss and disturbance from tourist industry; has also bred in S France, but only single (non-breeding) record from 20th century. Sparingly distributed in Morocco, where apparently declining; sparsely distributed but locally fairly common in Tunisia; possibly not widely distributed in Algeria. Loss of habitat to urbanization or agriculture probably biggest threat; nests in cultivated areas often at risk from agricultural activities; predation poorly documented, but in S Spain eggs and chicks may be taken by lizards (*Lacerta lepida*). On wintering grounds, uncommon in Morocco (Chichaoua region); probably not common in coastal areas of W Mauritania; uncommon in N Senegal; 9 road casualties recorded in Gambia since 1990, suggesting species previously overlooked there; widely distributed and reasonably common in Mali; few records Ivory Coast and Ghana; probably under-recorded. Increasing road traffic in all regions, responsible for some mortality.

Bibliography. Aragón (1996, 1997a), Aragón *et al.* (1998), Asensio *et al.* (1994), Badan & Kowalski (1998), Bannerman (1953), Barlow & Gale (1999), Barlow *et al.* (1997), Beven (1973), Christensen (1996), Copete & Gustamante (1992), Cowles (1967), Cramp (1985), Cuadrado & Domínguez (1996), Díaz, Asensio & Tellería (1996), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Eitchépar & Hue (1964), Finlayson & Tomlinson (1993), Forero, Tella & Gajon (1997), Forero, Tella & García (1995), Fry *et al.* (1988), Fuller (1995), Gargallo (1994), Gatter (1997), Grimes (1987), Hagemeijer & Blair (1997), Ledant *et al.* (1981), Mackworth-Præd & Grant (1970), Purroy (1997), Salewski (1997), Snow & Perrins (1998), Soares (1973), Thomsen & Jacobsen (1979), Tomás (1991).

49. Jungle Nightjar *Caprimulgus indicus*

French: Engoulevent jotaka **German:** Dschungelnachtschwalbe **Spanish:** Chotacabras de Jungla
Other common names: Indian Jungle Nightjar, Grey/Japanese Nightjar, (Ceylon) Highland Nightjar

Taxonomy. *Caprimulgus indicus* Latham, 1790. India.

Sometimes reckoned to be an eastern counterpart of *C. europæus*. Five subspecies recognized.

Subspecies and Distribution.

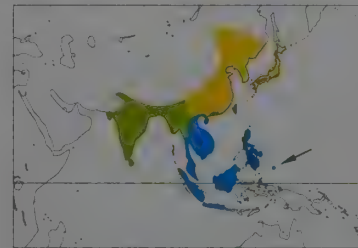
C. i. hazarae Whistler & Kinneir, 1935 - NE Pakistan E across Himalayas to NE India, Bangladesh and S China (Yunnan). S through Myanmar and Malay Peninsula.

C. i. indicus Latham, 1790 - India S of Himalayas (absent W Rajasthan and Kachchh).

C. i. kelaarti Blyth, 1852 - Sri Lanka.

C. i. jotaka Temminck & Schlegel, 1847 - SE Siberia, E. C & S China, Japan and Korea; winters from S China to Greater Sundas and Philippines.

C. i. phalaena Hartlaub & Finsch, 1872 - Palau Is.



Descriptive notes. 28–32 cm; male 60–108 g, female 65–92 g. Sexually dimorphic. Upperparts greyish-brown streaked blackish-brown, broadly so on crown; indistinct pale buff or tawny-buff nuchal collar; lesser coverts brown, speckled greyish-white, buff or tawny; rest of wing-coverts greyish-brown, boldly spotted greyish-white, pale buff or pale tawny with spots distinctly smudged or vermiculated brown; scapulars blackish-brown, broadly edged greyish-white vermiculated brown; buffish-white submoustachial stripe; large white patch on either side of lower throat; underparts greyish-brown, finely barred greyish-

brown or pale buff, becoming buff barred brown on belly and flanks. Male has four outer primaries with large white spot (inner web only on outermost one), and white tips to all but central pair of tail feathers; female has tawny wing spots and brownish-white or brownish-buff tips to tail feathers. Iris dark brown, bill brownish or blackish, legs and feet brownish. Larger than *C. asiaticus*, which has broad buff or tawny nuchal collar and much broader white tips to outermost tail feathers in male. Differs from both *C. macrurus* and *C. atripennis* by bold spotting on wing-coverts, and less broad white tips to two outermost tail feathers in male; from *C. manillensis* also by bold spotting on wing-

coverts, and that species shows buffish line across forewing. Larger than *C. affinis*, in which male usually has two outermost tail feathers entirely white. Immature similar to adult female. Races vary clinally in size and coloration: *hazarae* and *jotaka* larger and darker; *kelaarti* smaller and greyer, with more white markings; and *phalaena* smaller and perhaps more rufous. VOICE. Song of male is a rapid series of loud "tuk, tuk, tuk, tuk" notes, also a repetitive "tukoo, tukoo, tukoo" that occasionally ends with a hollow "wowowowow"; sings from perches, from ground and in flight. Calls include rapid sets of deep "quor" or soft "you" sounds. In Sri Lanka, flight call of male noted as "hóó, hóó, hóó hóóter".

Habitat. Mainly forest, woods and wooded country, in open woodland, deciduous, pine and mixed bamboo forest, glades and thick brush jungle; also open scrubland, farmland and cultivation, mandarin orange (*Citrus reticulata*) orchards and teak plantations. In Himalayas, also in sparsely vegetated ravines and on jungle-clad hillsides. In Sri Lanka, also occurs in stony fields. Wintering and passage birds have been recorded in large cities. Recorded from sea-level to 3300 m.

Food and Feeding. Feeds on moths, beetles, bugs, flying ants, cicadas, grasshoppers, locusts and small wasps. Foraging flight extremely agile and buoyant. Hunts close to ground, or high up over trees. Also feeds on insects attracted to artificial lights.

Breeding. Breeds late May to early Aug in Japan, Mar-Jun (mainly Apr-May) in Himalayas, late Apr to Jul in Pakistan, Feb-May (mainly Mar-Apr) in India, late Feb to Aug in S India, and Feb-Jul in Sri Lanka. Nest-site near or on rock, beneath vegetation, in thicket, on stony slope or in ravine; no nest, eggs laid on leaf litter, bare ground, or ashes following bush fires. Clutch 1-2 eggs, elliptical, creamy-white, spotted and marbled grey, brown and amber; incubation generally by female, male taking turns at dusk and dawn, period usually 16-19 days; chick covered in brown and buff down, fledges at c. 17 days.

Movements. Poorly understood. Throughout much of range from India E to S China, populations largely sedentary or locally migratory, some movements possibly altitudinal only. Races *kelaarti* in Sri Lanka and *phalaena* on Palau is probably sedentary. Race *jotaka* highly migratory: leaves breeding grounds Sept-Nov, moves S through E China, and possibly across South China Sea, to winter from S China, Indochina and Malaysia to Sumatra, Java, Borneo and Philippines. Japanese population possibly moves across Sea of Japan rather than East China Sea. Return migration probably Mar-May. Vagrants, possibly of migratory race *jotaka*, recorded in N Moluccas (Halmahera Is.), NW New Guinea (Manokwari, Irian Jaya) and Aleutian Is (Buldir Is).

Status and Conservation. Not globally threatened. Locally common summer visitor in NE Pakistan; common in India, where resident in many regions, locally migratory in others; locally common in Sri Lanka (perhaps commoner in E); fairly widespread throughout much of China; local but not uncommon summer visitor to Japanese islands of Kyushu, Shikoku, Honshu and Hokkaido; locally common to abundant in E and SE parts of Russia; fairly common passage migrant and winter visitor throughout Malaysia; rare winter visitor in Philippines; widespread winter visitor in Borneo, possibly more regular at higher altitudes. Adaptable, often occupying areas of deforestation and cultivation.

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50. European Nightjar

Caprimulgus europaeus

French: Engoulevent d'Europe German: Ziegenmelker Spanish: Chotacabras Europeo
Other common names: (Eurasian) Nightjar, Common Nightjar

Taxonomy. *Caprimulgus europaeus* Linnaeus, 1758, Sweden.

Forms superspecies with *C. fraenatus* and *C. rufigena*. Sometimes reckoned to be replaced to east by *C. indicus*. Much of geographical variation is clinal. Six subspecies recognized.

Subspecies and Distribution.

C. e. europaeus Linnaeus, 1758 - N & C Europe E through NC Asia (mainly S of c. 60° N) to L Baikal region.

C. e. meridionalis Hartert, 1896 - NW Africa and Iberia E through S Europe, Crimea, Caucasus and Ukraine to NW Iran and Caspian Sea.

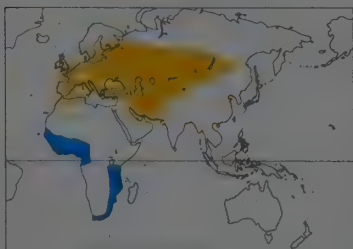
C. e. sarudnyi Hartert, 1912 - Kazakhstan, from Caspian Sea E to Kyrgyzstan, Tarbagatai and Altai.

C. e. uniwini Hume, 1871 - Iraq and Iran E to W Tien Shan and Kashgaria, N to S Turkmenistan and Uzbekistan.

C. e. plumipes Przewalski, 1876 - NW China and W & NW Mongolia.

C. e. dementievi Stegmann, 1949 - NE Mongolia and S Transbaikalia.

Winters in sub-Saharan Africa.



markings. Iris dark brown, bill blackish, legs and feet brown or flesh-brown. Smaller and darker brown than *C. ruficollis*, with white spots on primaries closer to wingtip. Larger than *C. rufigena*, with nuchal collar far less distinct. Paler and generally larger than *C. fraenatus*, which is more heavily spotted, and has broad buff or tawny-buff nuchal collar. Immature similar to adult female. Racial variation is generally clinal, birds becoming smaller and paler to E through range, with white wing spots of males becoming larger. VOICE. Song of male is a distinctive, continuous churring that frequently changes to a lower pitch and back again. Sings from perches and occasionally from ground. Contact call of both sexes, usually given in flight, is a short "co-ic"; bubbling trills are

given by male during interactions with female. A wide variety of calls given by both sexes include "chunk", "chink", "chik", "dak", "chuk", "chek", "chek-ek", "chuk" or clucking notes; at nest-site adult grunts or gives gruff "wuk, wuk, wuk" or muffled "oak, oak" notes; female also gives loud quacks. All birds make guttural hissing sounds during threat/defence displays. Chick utters a variety of chirps and cheeps.

Habitat. Mainly dry, open country: lowland heaths with scattered trees and bushes, commons and moorland, forest and woodland (especially glades, clearings and edges), recently felled woodland and young forestry plantations. Also chalk downland, industrial waste tips, wooded or scrub-covered steppe, sparsely forested or stony hillsides, oak scrubland, dense coppices, shingle, sand dunes, semi-deserts and deserts. Tends not to breed in urban areas, mountains, steppes, treeless plains, dense forest interior, mature plantations, cultivation and tall grassland, but not infrequently forages over such areas as farmland, gardens, reedbeds and wet habitats (e.g. marshes). On wintering grounds in wooded country, dry coastal acacia steppe, forest clearings, open sandy country and highlands. Recorded from sea-level to 2800 m on breeding grounds, up to 5000 m during winter.

Food and Feeding. Diet includes moths, beetles, mantises, mayflies, dragonflies, Orthoptera, cockroaches, bugs, Hymenoptera, antlions, lacewings, caddisflies and flies. Occasionally takes butterflies and flightless glow-worms, and also feeds on spiders and mites, latter probably taken with other prey items. Grit and small stones are also ingested and vegetable matter is probably taken accidentally. Foraging flight is agile and buoyant. Hunts over open country, in clearings, along woodland edges and borders, in woodland glades and rides, in gardens and orchards, over wetlands, in meadows and farmland, around grazing animals, and over stagnant ponds. Usually feeds solitarily, but loose feeding flocks sometimes occur. Also feeds on insects at artificial lights. May forage diurnally on overcast days. Also makes short flycatching sallies from ground or low perches, and hovers close to vegetation to take food from foliage. Occasionally hovers and swoops down after prey. Rarely feeds on ground, but does so by darting forward to take prey. Drinks in flight.

Breeding. Breeds late May to Aug, occasionally Apr-Jul in some regions; breeding often influenced by lunar phase. Single-brooded or double-brooded. Generally monogamous; territorial. Nest-site in open, beneath tree, bush or shrub, within upturned tree roots or among vegetation, occasionally inside mature plantation; sometimes used for several successive years; no nest, eggs laid on ground, on leaf litter, pine needles or bare soil. Clutch usually 1-2 eggs, elliptical, smooth and fairly glossy, whitish, greyish-white or cream, spotted and blotched yellow-brown, dark brown and grey or densely scrawled brown and grey, rarely unmarked, laid at intervals of 36-48 hours; incubation begins with first egg, mainly by female, period 17-21 days, eggs hatching asynchronously; chick semi-precocial, covered in dark brown and creamy-buff down, brooded by female for 10-16 days, then by male if female lays second clutch; female threatened at nest-site performs injury-feigning distraction display on ground, from exposed perch or in flight; young fledge at 16-17 days and become independent at c. 32 days. If two broods, female leaves first brood when chicks 10-16 days old; male then generally tends first brood and helps with second.

Movements. Highly migratory. Nominate race leaves breeding grounds late Jul to Nov (mainly late Aug to Oct), W populations moving S on broad front across Europe, Mediterranean and N Africa, E populations moving SW on broad front through Middle East (mid-Aug to early Dec) and E Africa. Winters mainly in E & S Africa, although small numbers may winter in W Africa. In spring, returning birds move N or NE, Mar-Jun, generally returning to breeding grounds Apr-May. Race *meridionalis* moves S on broad front across Mediterranean, N parts of Middle East and N Africa, and winters mainly in S and perhaps C Africa, though small numbers may winter in W Africa. Return movements probably at same time as nominate race. Race *sarudnyi* possibly winters mainly in E & SE Africa. In spring, moves NE through Arabian Peninsula, perhaps late Feb to May. Race *unwini* leaves breeding grounds possibly Aug-Sept and moves SE on broad front across Middle East; winters mainly in E & SE Africa, although small numbers occasionally overwinter in Israel, Pakistan and possibly NW India. Return route in spring apparently farther N. After breeding, race *plumipes* moves SW on broad front and winters mainly in SE Africa. Race *dementievi* probably also winters in E & SE Africa. Vagrants recorded in Iceland, Faeroes, Azores, Madeira, Canary Is and Seychelles.

Status and Conservation. Not globally threatened. Locally common to very common in suitable habitat throughout breeding range, though decreasing in numbers and/or range in many regions, especially in NW Europe. Total European breeding population estimated at 290,000-830,000 pairs, most in Russia (up to 500,000 pairs), Spain (up to 112,000 pairs) and Belarus (up to 60,000 pairs). Throughout range, breeding densities vary from 0.1 pair per km² to 19.4 pairs per km²; territory size variable, 1.5-31.9 ha. In Europe, major declines noted in late 19th century and these have continued through current century, most notably since 1970's, in Britain and Ireland, France, Belgium, Luxembourg, Netherlands, Denmark, Sweden, Finland, Czech Republic, Austria, Switzerland, Spain, Italy, Albania, Romania, Croatia, Bulgaria, Ukraine and Moldova; contraction of range also recorded in Andorra, Portugal and possibly Denmark; numbers also declining in Norway, Germany, Estonia, Latvia and Greece. Decreases probably due to reduction of insect availability resulting from pesticide use, increasing road traffic, disturbance at breeding sites, and loss or degradation of habitat, although in some countries, e.g. Britain, creation of habitat through commercial forestry has seen increase in numbers in recent years, though habitats not permanent and stability of higher population levels not guaranteed. Numerous predators, especially of eggs and chicks, include crows (*Corvus*), Magpies (*Pica pica*), Jays (*Garrulus glandarius*), owls (Strigidae), Sooty Falcon (*Falco coloratus*), hedgehogs (*Erinaceus europaeus*), weasels (*Mustela nivalis*) and domestic dogs. In Pakistan, a widely distributed and common breeding bird and passage migrant, a few birds possibly overwintering occasionally. On African wintering grounds, often common in SW Mauritania, probably under-recorded in NW Senegal, decreased in Gambia since early 20th century, rare in Ghana, fairly common in E Nigeria and S Cameroon, but very few records from other W African countries. Not uncommon in much of SE African range from Kenya (passage migrant only) and Tanzania S to Natal, though fairly common locally in Mozambique; widely distributed, especially in SE low veld, but possibly not common in Zimbabwe; scarce in Zambia.

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& Crick (1996), Pette (1982), Pinto (1983), Porter, Christensen & Schierner-Hansen (1996), Purroy (1997), Ravenscroft (1989), Richardson (1990), Roberts (1991), Rogacheva (1992), Rutgers & Norris (1972), Sachslehner & Schmalzer (1994), Schlegel (1967, 1969), Shirihai (1996), Sierr (1991), Silva & Reino (1996), Snow & Perrins (1998), Soares (1973), Stafford (1962), Stein (1982), Stepanyan (1990), Steyn (1996a), Tate (1989), Vaurie (1960b), de Wavrin (1990), Wright (1984), Zhao Zhengjie (1995), Zimmerman, D.A. *et al.* (1996).

51. Sombre Nightjar

Caprimulgus fraenatus

French: Engoulevent sombre **German:** Zügelnachtswalbe **Spanish:** Chotacabras Oscuro
Other common names: Dark Nightjar, Dusky Nightjar(!)

Taxonomy. *Caprimulgus fraenatus* Salvadori, 1884, Daimbi, Shoa.

Formerly considered conspecific with *C. rufigena*, and these two form superspecies with *C. europaeus*. In past, birds of Kenya occasionally separated as race *keniensis*, but probably not sufficiently distinct. Monotypic.

Distribution. Patchily from Ethiopia and NW Somalia S to NE Tanzania.



Descriptive notes. 25 cm; male 55-71 g, female 46-68 g. Sexually dimorphic. Upperparts dark brown, speckled greyish-white and streaked blackish-brown; broad buff or tawny-buff nuchal collar; wing-coverts dark brown, heavily spotted tawny and buff; scapulars irregularly marked blackish; white submoustachial stripe and white throat patch; underparts dark brown spotted buff, becoming buff barred brown on belly and flanks. Male has large white spot on four outermost primaries and broad white tips to two outermost tail feathers; female has pale buff wing spots and buff tips to tail. Iris dark brown, bill black, legs and feet

brown. More heavily spotted on wing-coverts and breast than *C. rufigena*, which is greyer and paler with streaked upperparts. Generally smaller than *C. europaeus*, which is paler with indistinct or no nuchal collar and shows buff line across wing-coverts; male of that species has smaller white wing and tail spots, female lacking white. Immature of present species similar to adult but browner and paler. Voice. Song of male is a low, evenly pitched, churr, occasionally interrupted by "kik-wow", "a-whoop" or liquid "kow" notes; sings from perches and possibly also from ground. Flight call is a liquid "quik" note; utters a throaty hiss during threat/defence displays.

Habitat. Typically open, stony bushland and scrubland; also grassland, sage bush, *Dodonaea* scrub and eucalyptus plantations. Recorded from sea-level to 3200 m.

Food and Feeding. Feeds on moths, grasshoppers, bugs and beetles. Forages by hawking for insects.

Breeding. Breeds May to perhaps Jul in NW Somalia, Feb-May and Nov in W Kenya, Jan-Mar and Sept-Nov in Ethiopia, C & S Kenya and NE Tanzania, and possibly Jun (though status unclear and breeding not proven) in SW Somalia and coastal Kenya. Probably monogamous. No nest, eggs laid on bare earth or sandy ground, usually among grass, often partly sheltered by shrubs or bushes. Clutch 1-2 eggs, elliptical or elliptical-ovate, pinkish-white, pinkish-buff or possibly glossy white, faintly spotted and blotched brown, lilac and grey, markings denser around blunt end; incubation usually by female, at least during day; female threatened at nest-site may give injury-feigning distraction display.

Movements. Generally sedentary, though locally migratory in parts of range. Small population occurs as breeding visitor (May-Oct) in NW Somalia and winters in Ethiopia. Outside normal breeding range, also recorded SW Somalia and N & E Kenya, and as a possible vagrant in Zaire (Ruwenzori), Burundi (Bujumbura) and S Tanzania (Njombe highlands).

Status and Conservation. Not globally threatened. Few data available; may be locally common in suitable habitat. Uncommon in extreme SE Sudan; not uncommon locally in NW Somalia; widespread and locally fairly common in W & S Kenya, where present in Tsavo West and Tsavo East National Parks; widely distributed and possibly fairly common in NE Tanzania.

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52. Rufous-cheeked Nightjar

Caprimulgus rufigena

French: Engoulevent à joues rousses **Spanish:** Chotacabras Carirrojo
German: Rostwangen-Nachtschwalbe

Taxonomy. *Caprimulgus rufigena* A. Smith, 1845, Eastern Cape Province, South Africa.

Formerly considered conspecific with *C. fraenatus*, and these two form superspecies with *C. europaeus*. In past, birds of Angola occasionally separated as race *quanzae*, but probably not distinct from nominate. Two subspecies currently recognized.

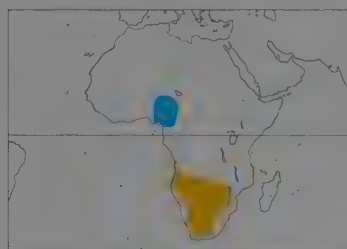
Subspecies and Distribution.

C. r. damarensis Strickland, 1852 - coastal W Angola, Namibia (except coastal region), Botswana and NW South Africa.

C. r. rufigena A. Smith, 1845 - South Africa, Zimbabwe and S Zambia; possibly also S Mozambique and S Angola.

Winters mainly in Nigeria and Cameroon.

Descriptive notes. 23-24 cm; male 48-65 g, female 46-66 g. Sexually dimorphic. Upperparts greyish-brown streaked blackish-brown; narrow buff or tawny-buff nuchal collar; wing-coverts greyish-brown, spotted tawny and buff, with broad buff line along scapulars; white throat patch; underparts greyish-brown spotted buff, becoming buff barred brown on belly and flanks. Male has large white spot on four outermost primaries and white tips to two outermost tail feathers; female has smaller white wing spots, usually tinged tawny, and buff tips to two outermost tail feathers. Iris brown, bill blackish, legs and feet brownish-flesh. Generally smaller than *C. europaeus*, which has indistinct or no nuchal collar and shows buff line across wing-coverts, female lacking white on wings and tail. *C. fraenatus* is darker and more heavily spotted; male has broader white tips to two outermost tail feathers; female has larger pale buff wing spots and broader buff tips to two outermost tail feathers. Immature of present species similar to adult but paler. Race *damarensis* is paler and greyer with upperparts more thinly streaked. Voice. Song of male is a continuous, evenly pitched churr, often



commencing with "a-whoop" notes and ending with low-pitched "kow" calls. Sings from ground or perches, mainly at dusk and dawn. Flight and alarm calls consist of "chuk" notes.

Habitat. Mainly open wooded savanna, miombo woodland, woodland edges and clearings, semi-arid acacia scrubland and semi-deserts; also in plantations and on sparsely vegetated hillsides. Recorded from sea-level to 1600 m.

Food and Feeding. Feeds on moths, beetles and other insects. Foraging methods not fully documented, although large numbers of birds may congregate where food supply is plentiful.

Also feeds on insects attracted to artificial lights.

Breeding. Breeds Sept-Nov in Angola and Zambia, Sept-Jan in Botswana, and Sept-Dec in Zimbabwe and South Africa. Monogamous; territorial. Nest-site partially shaded or in open, in burnt area, dry woodland, or occasionally damp vleis, recently felled woodland or open agricultural country; no nest, eggs often laid on bare earth, tends to avoid dense leaf litter. Clutch 1-2 eggs, elliptical, glossy, whitish, buffish or pale pinkish-cream, faintly but densely spotted and blotched brown, grey and lilac, occasionally unmarked; incubation period generally 15-17 days, beginning with first egg; chick covered in greyish-white and rufous down, fledges within 18-20 days.

Movements. A breeding visitor to much of S & SW Africa, after which moves N to winter in WC Africa. Main wintering range apparently in Cameroon (Apr-Aug) and less commonly Nigeria (May-Aug). May also winter in W Congo basin. Occurs as passage migrant in Zimbabwe, Zaire (whole country on N migration, W parts only on S migration), N Zambia, N Angola, Congo and Gabon. Also recorded as probable vagrant in Central African Republic and W Sudan (Darfur).

Status and Conservation. Not globally threatened. Frequent to locally common in suitable habitat during breeding season. Few data available on population levels; in S Zambia, common in Choma region, possibly scarce at all other localities; widespread in Zimbabwe, mainly on high veld; widely distributed and fairly common in most regions in Botswana; widespread and fairly common in South Africa, though apparently absent from much of E coast and from Natal; absent from coastal areas of W Namibia. On wintering grounds, frequent but widely distributed in wooded country, especially in Cameroon; rare in Nigeria, where only occasionally recorded at 1-4 localities; local and rare in Darfur region of Sudan. Present in several protected areas, including Kafue National Park (S Zambia), Hwange National Park (SW Zimbabwe) and Etosha National Park (Namibia).

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53. Egyptian Nightjar

Caprimulgus aegyptius

French: Engoulevent du désert **German:** Pharaonenziegenmelker **Spanish:** Chotacabras Egipcio

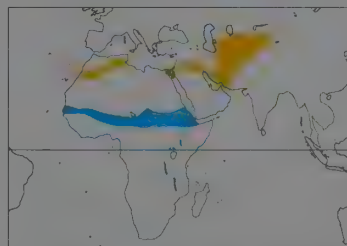
Taxonomy. *Caprimulgus aegyptius* Lichtenstein, 1823, upper Egypt.

Asian populations (E of Syria) sometimes separated as race *arenicolor*, but variation is clinal, with birds increasing in size towards east. Two subspecies recognized.

Subspecies and Distribution.

C. a. saharae Erlanger, 1899 - C & EC Morocco, N (and occasionally S) Algeria, C Tunisia, probably NW Libya, and possibly E towards N Egypt; winters in W Sahel.

C. a. aegyptius Lichtenstein, 1823 - NE Egypt and N Arabian Peninsula, E to extreme CW China, NE Kazakhstan, Tajikistan, extreme W Pakistan and SE Iran; winters in E Sahel.



Descriptive notes. 24-26 cm; male 68-93 g, 1 female 70 g. Sexually dimorphic, though not greatly so. Upperparts sandy-grey or greyish-buff, lightly spotted blackish-brown; indistinct buffish nuchal collar; wing-coverts sandy-grey or greyish-buff, speckled and vermiculated brown and blackish brown and boldly spotted buff, no scapular pattern; buffish-white submoustachial stripe and white throat patch; underparts sandy-grey or greyish-buff, spotted buff and barred brown, becoming buff barred brown on belly and flanks. Both sexes generally lack white wing spots (although some show a small white spot towards wing

tip) but have white underwings. Male has narrow whitish tips to two outermost tail feathers; female has pale buffish tips. Iris dark brown, bill blackish or dark brown, legs and feet blackish, greyish or brownish. Larger than *C. maharattensis*, which has white wing spots; and male has broad white tips to two outermost tail feathers, female having narrow buffish-white tips. Immature of present species similar to adult but paler and plainer. Race *saharae* is sandier and slightly smaller. Voice. Song of male is a long series of purring "kowr" notes; sings from ground, mainly at dusk and dawn. Birds also utter short churrs, "tuk-l, tuk-l", "chuc, chuc", croaking "toc" and growling "owk" calls.

Habitat. Typically deserts and semi-deserts, often close to water; also arid plains of sand or clay with scattered scrub and tamarisks, and dry waste ground near water. In wintering area in Sudan, also found in long grass among trees. Race *saharae* breeds in deserts, desert-steppe, or sandy steppe with limestone outcrops, and winters in dry country with *Salsola*, *Artemisia* and tamarisks, or among rice fields.

Food and Feeding. Diet includes beetles, bugs, moths, crickets, grasshoppers, ants, termites and mosquitoes. Forages low over ground near wells and bushes, over water and among livestock; also over cultivated land and towns. Small feeding flocks occasionally noted. Drinks in flight, by dipping bill into surface of water.

Breeding. Breeds mid-Mar to Jun in Morocco (longer in wet years), mid-Apr to mid-Jun in Algeria and Tunisia, and from mid-May in Turkmenistan. Possibly double-brooded. Nest-site among stones, sheltered by small bushes, in open, or in depression in ground; no nest, eggs laid on ground. Clutch 1-2 eggs, elliptical, smooth or glossy, cream or whitish, marbled and blotched pale olive and grey; incubation beginning with first egg, mainly by female, period c. 17-18 days,

eggs usually hatching asynchronously; chick semi-precocial, covered in pale buff or sandy-buff down, fledges in c. 4 weeks.

Movements. Nominate race migratory in much of range, partially sedentary in Egypt. Leaves breeding grounds by Sept and migrates on broad front, SE across Arabian Peninsula (Sept-Nov). Small numbers may overwinter in Arabia, but main wintering range in E Sahelian zone of Africa. Recorded NE & SE Egypt, C & NE Sudan (Oct-Mar), N & NE Chad, and NE Nigeria. Rarer N & C Ethiopia (Dec-Jan), NW Somalia (one Dec record), E Mali (Jan-Apr) and N Togo (possibly vagrant, May-Jun). Return movements late Feb to early Jun (mainly mid-Mar to mid-May). Race *saharae* migratory, leaving breeding grounds Sept-Oct and moving S & SW. Wintering range in W Africa, from S Mauritania (Sept-Feb) and N Senegal (Dec-Feb) through C & SC Mali (Nov-Feb) to N Burkina Faso, SE Niger and NE Nigeria. Return movements Mar-Apr. Vagrants recorded in Britain, Sweden, Germany, Italy, Sicily, Malta and Cyprus.

Status and Conservation. Not globally threatened. Widespread from Tarfaya to Taouz in Morocco; formerly common in Tunisia but now apparently scarce; locally scarce to common in Egypt. Apparently disappeared from Israel as a breeding species by 1940's, possibly because of loss of habitat to agriculture and urban construction, although a few birds occasionally summer and may therefore attempt breeding. Formerly common in Iraq but now possibly rarer; possibly common to locally abundant in S & E Iran, Baluchistan, Afghanistan, Turkestan and N & S Tadjikistan; scarce summer visitor to W edges of Chagai, Pakistan, though possibly under-recorded. In winter, locally uncommon to common in S Mauritania (Nouakchott region); fairly common but local in N Senegal (at Richard Toll); probably not uncommon locally in NE Nigeria; sparsely distributed but locally common in C & S Mali; widespread but sparsely distributed and generally uncommon in Sudan (N of L No). No data available from other regions.

Bibliography. Abdulali & Hussain (1972a), Ashford & Bray (1977), Baha el Din (1995), Bakaev & Norov (1990), Bannerman (1953), Barlow *et al.* (1997), Cave & Macdonald (1955), Cowan (1982), Cramp (1985), Dementiev & Gladkov (1951), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Dupuy (1970), Elgood, Fry & Dowsett (1973), Elgood, Heigham *et al.* (1994), Échécopar & Hùe (1964), Evans (1994), Flint *et al.* (1984), Fry *et al.* (1988), Goodman *et al.* (1989), Grimmett *et al.* (1998), Hùe & Échécopar (1970), Jackson (1985c, 1986), Knystautas (1993), Ledant *et al.* (1981), Lyngs (1986), Mackworth-Praed & Grant (1957, 1970), Nikolaus (1989), Paz (1987), Porter, Christensen & Schierner-Hansen (1996), Roberts (1991), Robin (1969), Shirihai (1996), Snow & Perrins (1998), Sopyev (1967), Stepanyan (1990), Swash & Cleere (1989), Symens *et al.* (1992), Vaurie (1960b), Zhao Zhengjie (1995).

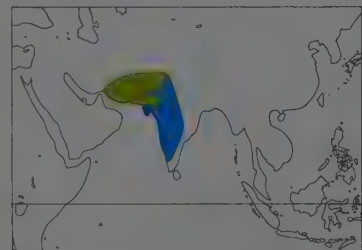
54. Sykes's Nightjar

Caprimulgus mahrattensis

French: Engoulevent de Sykes **German:** Sykesnachtschwalbe **Spanish:** Chotacabras Mahratta
Other common names: Sind Nightjar

Taxonomy. *Caprimulgus Mahrattensis* Sykes, 1832, Mahrattas.
Monotypic.

Distribution. SE Iran, S Afghanistan, Pakistan and possibly NW India. Winters in W & C India.



tips. Iris dark brown, bill dark brown, legs and feet pale fleshy-brown. Smaller than *C. aegyptius*, which generally lacks white wing spots, although underwings are white; male of that species has narrow buffish-white tips to two outermost tail feathers, female having buffish tips. Immature paler and plainer than adult. **VOICE.** Song of male is an evenly pitched churr given from ground, mainly at dusk and dawn. Calls include soft "chuk-chuk" or "cluk-cluk" notes.

Habitat. Mainly semi-deserts with scattered thorn scrub; also dry stony scrubland, gravel or clay plains, flat salty ground with tamarisks, and stony wasteland. Occasionally found in dry hilly areas with rocky outcrops, and sparsely vegetated sand dunes in deserts. Tends to avoid cultivation. Lowland species, recorded from sea-level to 500 m.

Food and Feeding. Feeds on moths, beetles and other insects. Foraging flight agile and buoyant, and hunts low over open country, including swamps.

Breeding. Breeds Feb-Aug (mainly Mar-May) in Pakistan and possibly Feb-Jun in NW India (Punjab); no data from other regions. Possibly semi-colonial at times. Nest-site in full sunlight, or sheltered beneath clump of grass or small bush, e.g. tamarisk or bramble; no nest, eggs laid on bare, stony or salt-encrusted ground. Clutch 2 eggs, elliptical, greyish-white, smeared and blotched grey; incubation usually by female, period c. 17-18 days; chick semi-precocial, covered in grey and black speckled down.

Movements. Poorly known. Sedentary and partially migratory. After breeding season, disperses widely and winters throughout W & C India, where recorded from Rajasthan, Kutch, N Gujarat, Saurashtra, W Khandesh, Deccan and Konkan S to N Mysore.

Status and Conservation. Not globally threatened. Locally common in many regions within breeding range, widely but sparsely distributed in winter. Widespread and common in Pakistan, where mainly resident, but breeding visitor only to foothills of Salt Range, Thal and lower Kurram Valley. Present in Khirtar National Park, 80 km NW of Karachi.

Bibliography. Abdulali & Hussain (1971b), Ali & Ripley (1983), Daniels (1997), Evans (1994), Grimmett *et al.* (1998), Hollom *et al.* (1988), Hùe & Échécopar (1970), Kalsi (1998), Kazmierczak *et al.* (1998), Mukherjee (1995), Porter, Christensen & Schierner-Hansen (1996), Ripley (1982), Roberts (1991).

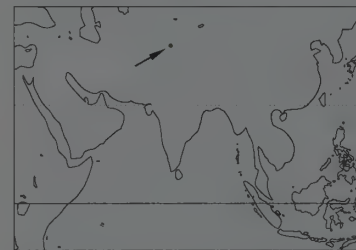
55. Vaurie's Nightjar

Caprimulgus centralasicus

French: Engoulevent de Vaurie **German:** Vaurienachtschwalbe **Spanish:** Chotacabras de Vaurie
Other common names: Central Asian Nightjar, Chinese/Xinjiang Nightjar

Taxonomy. *Caprimulgus centralasicus* Vaurie, 1960, Pishan, western Xinjiang, western China. Taxonomic status perhaps questionable. Known only from type specimen, an immature female originally identified as *C. aegyptius*, and compared only with that species when described; further study of immature *C. europaeus plumipes* may also be of interest. Monotypic.

Distribution. W China (SW Xinjiang), where possibly occurs throughout S Tarim basin along Kun Lun.



Descriptive notes. 19 cm. Known only from type specimen, an immature female. Upperparts sandy-buff, streaked and vermiculated brown, no nuchal collar; wing-coverts sandy-buff vermiculated brown and spotted pale buff, scapulars buff with dark central streaks; underparts pale buffish barred brown; underwing buffish but lacks white markings on wings; two outermost tail feathers narrowly tipped pale buffish-white. Iris dark brown, bill dark horn, legs and feet fleshy-brown. Smaller than *C. aegyptius*, which is slightly greyer and more spotted, with darker underwings and white underwings. Immature plumages unknown, although the only known specimen could perhaps be of an immature bird. **VOICE.** Unknown.

Habitat. Possibly arid plains and sandy foothills covered in short scrub.

Food and Feeding. Unknown.

Breeding. No information.

Movements. Unknown.

Status and Conservation. **VULNERABLE.** Restricted-range species; present in Taklimakan Desert EBA. Taxonomic status of species is perhaps questionable. Known only from type specimen, an immature female taken from Pishan (Guma) in SW Xinjiang, W China, in Sept 1929. Habitat in region of type locality has been severely damaged in recent years by grazing and trampling of livestock, cultivation and irrigation, and collection of timber for firewood. Recent surveys in 1970's and 1990's have so far failed to find this species and only *C. europaeus* has been located.

Bibliography. Collar & Andrew (1988), Collar *et al.* (1994), Duff (1994), Échécopar & Hùe (1978), Inskipp *et al.* (1996), Meyer de Schauensee (1984), Stattersfield *et al.* (1998), Vaurie (1960a), Zhao Zhengjie (1995).



ssp nubicus



56



57



ssp torridus



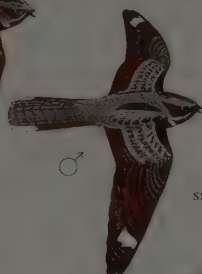
ssp tamaricis



ssp albonotatus



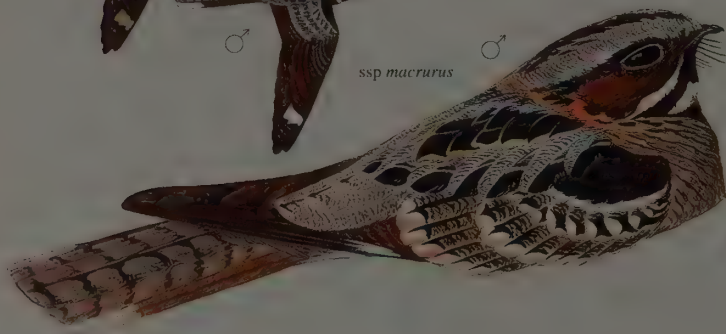
♀



♂

ssp macrurus

♂



58

ssp schlegelii

♂



♀



♂

59



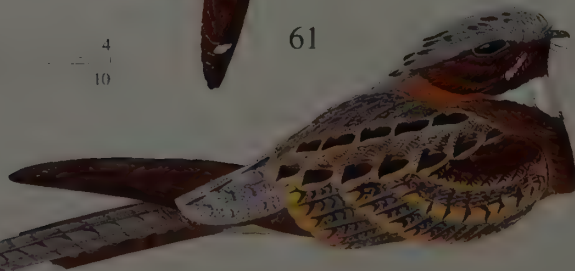
60



61

inches
cm

4
10



♂

rufous bird



♂

62



♂

dark bird

56. Nubian Nightjar

Caprimulgus nubicus

French: Engoulevent de Nubie **German:** Nubischer Ziegenmelker **Spanish:** Chotacabras Nubio

Taxonomy. *Caprimulgus nubicus* Lichtenstein, 1823, Nubia.

Birds from desert regions between Mt Kilimanjaro and Tsavo formerly placed in race *taruensis*. Four subspecies currently recognized.

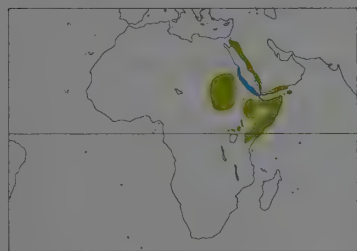
Subspecies and Distribution.

C. n. tamaricis Tristram, 1864 - Israel and Jordan S to SW Saudi Arabia (including one record from Farasan Is) and SW & S Yemen; some birds winter in coastal Sudan and Eritrea to NW Somalia.

C. n. nubicus Lichtenstein, 1823 - C Sudan.

C. n. torridus Lort Phillips, 1898 - Somalia, C Ethiopia, Kenya and possibly NE Uganda.

C. n. jonesi Ogilvie-Grant & Forbes, 1899 - Socotra.



Descriptive notes. 21-22 cm; male 46-55 g, 1 female 49 g. Upperparts greyish or buffish, thinly streaked blackish-brown, with crown often heavily streaked or spotted rufous; broad tawny-buff nuchal collar; wing-coverts and scapulars lightly spotted buff or heavily spotted tawny and buff; white throat patch; underparts buff barred brown. Male has large white spot on four outermost primaries and broad white tips to two outermost tail feathers; female has smaller wing and tail spots. Iris dark brown, bill dark brown, legs and feet brownish or greyish. Differs from *C. clarus* by shorter tail, and tawny or buff spotting on upperparts; also lacks

the well-marked pattern on inner wing of that species. Immature plainer and paler than adult, but otherwise similar. Races vary in coloration, amount of spotting on upperparts and wing-coverts, and extent of white on two outermost tail feathers. Voice. Song of male is a double-noted "ow-wow" or treble-noted "ow-wow-wow", given from ground.

Habitat. Typically dry, sparsely vegetated wadis, acacia scrubland (often near water), tamarisk thickets, dried riverbeds with some water, desert thorn scrub, sandy scrubland, bushy coastal dunes and possibly salt-marshes. In Yemen, also in climax acacia/euphorbia woodland. Recorded from sea-level to 1000 m, rarely to 1650 m.

Food and Feeding. Diet includes moths, grasshoppers and beetles. Forages by flitting about after prey, often hunting close to water. Also forages on ground, especially among animal droppings.

Breeding. Poorly known. Breeds Apr to perhaps Jul in Jordan and Israel, May (possibly) to Sept in Saudi Arabia (juvenile late Sept), Jun-Aug in NW Somalia (juvenile Aug) and late Mar to May in S Kenya. No nest, eggs laid on bare soil, sand or gypsum, often at base of small thorn bush. Clutch 1-2 eggs, elliptical, ivory-white or dull white, marbled or blotched lilac and brown.

Movements. Poorly known. Nominate race probably sedentary. Middle Eastern race *tamaricis* possibly sedentary and partially migratory. Some may move SW during Oct-Nov to winter in coastal lowlands of NE Sudan, Eritrea, Djibouti and NW Somalia. Autumn vagrants also recorded NE Saudi Arabia and Oman (mainly Oct). Return movements in spring noted mid-Feb to late May (mainly Mar-Apr) in Israel. Race *torridus* possibly sedentary and partially migratory. Socotran race *jonesi* probably sedentary.

Status and Conservation. Not globally threatened. Locally common in EC Sudan, C Ethiopia and N Somalia (Haud Plateau); widely distributed but uncommon and local in Kenya, where status uncertain and possibly a migrant only; scarce in Israel, Jordan, SW Saudi Arabia and coastal regions of Yemen; probably not common on Socotra Is, though possibly under-recorded. Decline in Israel noted since 1980's, population possibly reduced to no more than 15-20 breeding pairs and on brink of extinction, probable causes being loss of habitat, use of pesticides in farming, and increased road mortalities.

Bibliography. Archer & Godman (1937-1961), Ash & Miskell (1983b, 1998), Britton (1980), Brooks *et al.* (1987), Cave & Macdonald (1955), Cramp (1985), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Dowsett *et al.* (1977), Evans (1994), Fry *et al.* (1988), Gallagher & Rogers (1980), Gallagher & Woodcock (1980), Goodman *et al.* (1989), Hollom *et al.* (1988), Húe & Étchécopar (1970), Jennings (1995), Kirwan *et al.* (1996), Lewis & Pomeroy (1989), Mackworth-Præd & Grant (1957), Nikolaus (1987), Paz (1987), Peters & Loveridge (1936), Porter, Christensen & Schiermacker-Hansen (1996), Porter, Martins *et al.* (1996), Shirihai (1996), Short *et al.* (1990), Smith (1957), Snow (1978), Swash & Cleere (1989), Symens *et al.* (1992), Urban & Brown (1971), Zimmerman, D.A. *et al.* (1996).

57. Golden Nightjar

Caprimulgus eximius

French: Engoulevent doré **German:** Prachtnachtschwalbe **Spanish:** Chotacabras Dorado

Taxonomy. *Caprimulgus eximius* Temminck, 1826, Sennar, Sudan.

Two subspecies recognized.

Subspecies and Distribution.

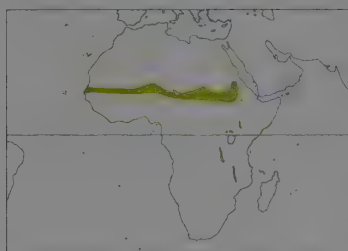
C. e. simplicior Hartert, 1921 - S Mauritania and N Senegal E to C Chad.

C. e. eximius Temminck, 1826 - C Sudan.

Descriptive notes. 23-25 cm; 1 male 66 g. Sexes similar. Upperparts and wing-coverts tawny or tawny-buff, with greyish-white rectangular spots edged and densely speckled dark brown; no nuchal collar; large white throat patch; underparts similar to upperparts, becoming paler and unmarked on lower breast and belly. Both sexes have large white spot on four outermost primaries and broad white tips to two outermost tail feathers. Iris, bill, legs and feet all greyish-black. Immature similar to adult but paler and plainer. Race *simplicior* paler and buffier. Voice. Song of male is a prolonged churr given from ground.

Habitat. Typically, sparsely vegetated semi-desert with grass and scrub, in sandy, gravelly, stony or rocky country; also fallow cultivation. In N Senegal, also open, sandy country with scattered trees. Tends to avoid wooded areas and dense scrub. Lowland species, recorded from sea-level to 600 m.

Food and Feeding. Feeds on moths, grasshoppers, mantises, bugs and beetles. Forages at dusk, often close to or over water. Foraging methods poorly known.



Breeding. Poorly documented. Breeds Apr-May in N Senegal and Mali, Mar-Apr in Sudan; no data from other regions. No nest, eggs laid on bare ground, usually near vegetation or clump of grass. Clutch usually 2 eggs, ovate, greyish-white or greyish-buff, heavily blotched greyish or yellowish-brown over mauve; chick covered in rufous-isabelline down.

Movements. Generally sedentary, although in W of range race *simplicior* may disperse after breeding and undertake some local movements; occasionally strays farther afield, as vagrant recorded at Guellet du Zemmour in SW Morocco.

Status and Conservation. Not globally threatened. Uncommon, perhaps even rare, in N Senegal (rare in Djoudj National Park but more frequently recorded near Richard Toll), common in SW Mauritania (S of Nouakchott), fairly common and widespread in C Mali, and not uncommon in parts of Sudan. No data available from other regions.

Bibliography. Balança & de Visscher (1997), Bannerman (1953), Barlow *et al.* (1997), Brouwer & Mullié (1992), Cave & Macdonald (1955), Cleere (1995b), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Fry *et al.* (1988), Gee (1984), Giraudoux *et al.* (1988), Lamarehe (1980), Mackworth-Præd & Grant (1957, 1970), Morel & Morel (1990), Nikolaus (1987), Rodwell *et al.* (1996), Rothschild & Wollaston (1902), Snow (1978).

58. Large-tailed Nightjar

Caprimulgus macrurus

French: Engoulevent de Horsfield **Spanish:** Chotacabras Macruro

German: Langschwanz-Nachtschwalbe

Other common names: Long-tailed Nightjar (!)

Taxonomy. *Caprimulgus macrurus* Horsfield, 1821, Java.

Forms superspecies with *C. atripennis*, *C. manillensis* and *C. celebensis*, and all four were formerly considered conspecific. Race *schlegelii* includes possible races: *schillmolleri* (N Moluccas and W Papuan Is); *obiensis* (NC Moluccas); *mesophanis* (S Moluccas); *oberholseri* (W Lesser Sundas); *kuehni* (Kai and Tanimbar); *yorki* (Bismarck Archipelago to N Australia); and *meeki* (Louisiane Archipelago). In past, birds of SE Asia occasionally separated as race *ambiguus*, those of Hainan as race *hainanus*. Seven subspecies currently recognized.

Subspecies and Distribution.

C. m. albonotatus Tickell, 1833 - NE Pakistan and N & E India E to Bhutan and Bangladesh.

C. m. bimaculatus Peale, 1848 - NE India E to S China, and S to Sumatra and Riau Archipelago.

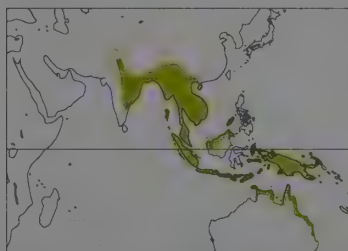
C. m. andamanicus Hume, 1873 - Andaman Is (possibly absent from Little Andaman).

C. m. johnsoni Deignan, 1955 - SW Philippines (Palawan and probably Calamian Group).

C. m. salvadorii Sharpe, 1875 - W & N Borneo (Sarawak, Brunei, Sabah), including Labuan, Balambangan and Banguay and S Sulu Is.

C. m. macrurus Horsfield, 1821 - Java and Bali.

C. m. schlegelii A. B. Meyer, 1874 - Wallacea, New Guinea and New Britain to coastal N & NE Australia.



Descriptive notes. 25-29 cm; male 54-79 g, female 60-72 g, unsexed 55-90 g. Sexually dimorphic. Upperparts greyish-brown streaked blackish-brown, broadly so on crown; indistinct buff or tawny-buff nuchal collar; wing-coverts greyish-brown, spotted buff or tawny-buff, with lesser coverts darker and scapulars blackish-brown, broadly bordered buff on outer webs; white submoustachial stripe and large white throat patch; underparts brownish, barred and speckled buff, becoming buff barred brown on belly and flanks. Male has large white spot on four outermost primaries and broad white tips to two outermost tail feathers; female has

buff wing spots and narrow buff or buffish-white tips to two outermost tail feathers. Iris dark brown, bill blackish, legs and feet blackish. Differs from *C. atripennis* by darker head and more streaking on crown; that species is more rufous on hindneck, mantle, back and breast; male has smaller white wing spots and female smaller buff spots. *C. manillensis* is smaller and more spotted and shows buffish line across wing-coverts; male has smaller white wing spots and narrower white tips to two outermost tail feathers, female often having buffish wing spots. *C. celebensis* has smaller white wing spots and narrower white tips to two outermost tail feathers. Immature of present species similar to adult but duller and tawnier. Races differ mainly in size and overall coloration. Voice. Song of male is a continuous chopping or knocking, "tok, tok, tok, tok", given from perches and ground and occasionally in flight. Calls include low grunts, croaks or growls; and in flight a treble-noted "chok-a-chok"; makes guttural hissing sounds during distraction displays.

Habitat. Varied, though often preferring areas with trees. Inhabits deciduous forests and woods, bamboo forests and thickets, monsoon and coastal forests, edges of rainforest, secondary forest and scrub, forest clearings, forested foothills, and thick bush; also in open country, savanna, mid-montane and other grasslands, disturbed habitats, suburban gardens, villages, cultivation and coffee estates, along roadsides, by broad forest rivers or dry stream beds, near beaches, on offshore islands and river sandbanks, and in mangroves, swamps and overgrown creeks. Recorded from sea-level to 2700 m in N parts of range, 0-2000 m in New Guinea, 0-1200 m in Borneo and Wallacea, and 0-900 m in Sumatra. In N Pakistan, birds arriving in summer occur between 460-900 m.

Food and Feeding. Diet includes moths, crickets, grasshoppers, wasps, earwigs, bugs and beetles. Forages by making flycatching sallies from perches or ground. Also hawks after prey or feeds on ground. Feeding range may cover c. 50 ha. Occasionally hovers near grazing livestock, preying on insects disturbed or attracted by them.

Breeding. Breeds Mar-May in N India and Myanmar, Mar-Jun in N Thailand, Mar-Apr in Andamans, Jan to perhaps Jun in Malay Peninsula, Jan-May in Sumatra, Jul on Palawan, up to Apr in Sarawak,

Sept-Feb in Java, Oct on Flores, Sept on Bacan, Sept-Jan in New Guinea (also Jul in W highlands), and Sept-Nov (occasionally Aug-Jan) in N & NE Australia. Probably single-brooded. In parts of range, may be loosely colonial; territorial. Nest-site beneath tree or bush, near stones, on lawn or grass, in open area, along forest and woodland edges, on hillside or on seashore, may be used for several years in succession; no nest, eggs laid on leaf litter, bare earth or sand. Clutch 1-2 eggs, elliptical or oval, glossy, whitish, cream, pale pinkish-cream or salmon-buff, indistinctly blotched and spotted grey, pale purplish-brown and lavender; incubation usually by female during day, period c. 16-22 days; adults threatened at nest-site perform injury-feigning distraction display; chick semi-precocial, covered in pinkish-buff down, speckled and mottled blackish, brooded for c. 14 days, independent at c. 35 days.

Movements. Poorly documented. Most populations appear to be mainly sedentary. Race *albonotatus* sedentary and partially migratory, e.g. summer breeding visitor to Pakistan, arriving from mid-late Mar and leaving again in Sept, when probably moves E. In other parts of range, less frequent Oct-Feb and may be subject to some local movements. Race *schlegelii* generally sedentary, but may undertake local movements in parts of range. In Australia, possibly occurs as a vagrant as far S as Queensland/New South Wales border.

Status and Conservation. Not globally threatened. Common to locally abundant throughout much of range. In NE Pakistan, scarce and local summer visitor only. Widely distributed throughout Andaman Is, though possibly absent from Little Andaman and absent from nearby Nicobar Is; locally common in W Malaysia. Widespread but locally uncommon to fairly common throughout Wallacea, though scarce at many localities and absent from others; fairly common on Palawan; locally common in Brunei and possibly also Sarawak and Sabah; possibly scarce in Sumatra; locally common in Java; widespread in Moluccas. Widely but patchily distributed in New Guinea where locally common to very common, and in some regions such as E Highlands quickly colonizes areas where forests have been cleared. In Australia, widely distributed in N & E, where not greatly threatened, although local populations may vacate areas where habitat degraded by trampling of large animals such as feral water buffalo (*Bubalus bubalis*).

Bibliography. Ali (1996), Ali & Ripley (1983), Ali *et al.* (1996), Beehler *et al.* (1986), Bell (1986), Beruldsen (1991), Betham (1938), Blakers *et al.* (1984), Campbell (1976), Catterall (1997), Coates (1985), Coates & Bishop (1997), Condon (1975), Davis (1979b), Deignan (1945), Diamond (1972), Diamond & LeCroy (1979), Dickinson *et al.* (1991), Duckett & Duckett (1982), Duckworth & Kelsh (1988), Eames & Ericson (1996), Étchécopar & Hùe (1978), Gilliard & LeCroy (1961), Grimmer *et al.* (1998), Hellebrekers & Hoogerwerf (1967), Higgins (1999), Holmes (1996, 1997), Holmes & Burton (1987), Inskipp (1995), Inskipp *et al.* (1996), Isherwood *et al.* (1997), Johnstone *et al.* (1996), Jones (1923), Lekagul & Round (1991), Lowther (1937), MacKinnon & Philipps (1993), Madoc (1976), van Marle & Voous (1988), Marshall (1978), Mayr & Rand (1937), McClure (1998), McLean (1983), McNab & Bonaccorso (1995), Medway & Wells (1976), Mees (1977a, 1982b, 1985b), Oberholser (1915a), Opt (1975), Osmaston (1921a), Rajathurai (1996), Rand & Gilliard (1967), Ripley (1964a, 1982), Ripley & Beehler (1987), Roberts (1991), Round (1988), Rowland (1995b), Saini & Saini (1995), Schodde & Mason (1981), Smythies (1981, 1986), Stepanyan (1995), Strahan (1994), Tikader (1984), Wells (1999), Whistler & Kinnear (1935), White & Bruce (1986), Wickham (1909), Zhao Zhengjie (1995).

59. Jerdon's Nightjar *Caprimulgus atripennis*

French: Engoulevent de Jerdon

Spanish: Chotacabras Marajá

German: Maharadschanachtschwalbe

Other common names: Long-tailed Nightjar(!), Indian Long-tailed Nightjar; Ceylon Nightjar (*aequalis*)

Taxonomy. *Caprimulgus atripennis* Jerdon, 1845, Eastern Ghats, India.

Forms superspecies with *C. macrurus*, *C. manillensis* and *C. celebensis*, and all four were formerly considered conspecific. Occasionally treated as monotypic. Two subspecies normally recognized.

Subspecies and Distribution.

C. a. atripennis Jerdon, 1845 - Western Ghats (Kerala N to S Maharashtra) and Eastern Ghats (Tamil Nadu N to Durgapur, West Bengal).

C. a. aequalis Ripley, 1945 - Sri Lanka.



Descriptive notes. 25.5-27 cm; 1 male 55 g. Sexually dimorphic. Crown greyish-brown, central feathers boldly but sparsely spotted or streaked blackish-brown; rest of upperparts greyish-brown tinged rufous; nuchal collar rufous, often ill-defined; lesser coverts dark brown speckled rufous, rest of wing-coverts greyish-brown, speckled and spotted buff; scapulars blackish-brown, with pale tawny bar across middle of each feather; underparts brownish speckled buff, cinnamon and rufous-buff, becoming buff barred brown on belly and flanks. Male has white spot on four outermost primaries and broad white tips to two outermost tail feathers. Female has buff wing spots and buff or buffish-white tips to two outermost tail feathers. Iris brown, bill dark brown, legs and feet dark brown. *C. macrurus* is greyer-brown with crown more heavily streaked blackish-brown; male has larger white wing spots, female larger buff spots. *C. asiaticus* is smaller with heavier streaking on crown, a tawny-buff nuchal collar and heavier tawny-buff spotting on wing-coverts. Immature of present species similar to adult but paler, with crown less heavily spotted. Race *aequalis* is darker, especially on upperparts. Voice. Song of male is a repetitive, liquid "ow-r-r-r", often preceded by low "grog" sounds; sings from perches, mainly at dusk and dawn.

Habitat. Mainly forest, woods and forested country; evergreen forest, moist deciduous forest, dry forest, mixed bamboo forest and second-growth forest; also coffee estates and wooded suburban areas. In Sri Lanka, also semi-cultivated country and scrubland, especially with trees or tracts of woodland. Recorded from sea-level to 2000 m.

Food and Feeding. Poorly documented. Feeds on insects, especially beetles, moths and termites. Forages in powerful, swooping flight, interspersed with frequent glides.

Breeding. Poorly studied. Breeds Mar-Jul (mainly Mar-Apr) in India, Feb-May and Aug-Sept in Sri Lanka. No nest, eggs laid usually on sandy ground, often close to or beneath shrub or bush. Clutch 2 eggs, elliptical, cream or buffish, sparsely spotted and speckled brown, dark brown and grey; sexes share incubation; chick semi-precocial, but not described.

Movements. None documented. Sedentary.

Status and Conservation. Not globally threatened. Reported to be reasonably common throughout its range, although details lacking. Occurs in several protected areas, including Rajiv Gandhi

(Nagarhole), Mudumalai and Indira Gandhi National Parks (India); also, in Sri Lanka, found in Uda Walawe and Yala National Parks, being common in latter.

Bibliography. Ali & Ripley (1983), Gauntlett (1995), Grimmer *et al.* (1998), Henry (1998), Inskipp (1995), Inskipp *et al.* (1996), Marshall (1978), Mees (1977a, 1985b), Phillips (1978), Ripley (1945, 1982), Ripley & Beehler (1987), Whistler & Kinnear (1935).

60. Philippine Nightjar *Caprimulgus manillensis*

French: Engoulevent des Philippines

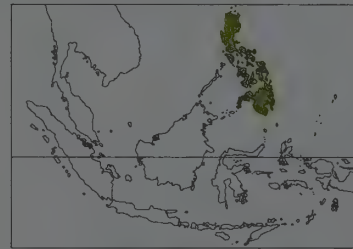
Spanish: Chotacabras Filipino

German: Philippinennachtschwalbe

Taxonomy. *Caprimulgus manillensis* Walden, 1875, Manila.

Forms superspecies with *C. macrurus*, *C. atripennis* and *C. celebensis*, and all four were formerly considered conspecific; in recent years has commonly been lumped with *C. celebensis*, but differs in both voice and morphology. Proposed race *delacouri* for Mindanao birds is not distinct. Monotypic.

Distribution. Philippines (except SW).



Descriptive notes. 23-25 cm; male 59-68 g, female 58-71 g. Sexes similar. Upperparts greyish-brown streaked blackish-brown, broadly so on crown, with no nuchal collar; indistinct buffish line across wing-coverts; lesser coverts dark brown flecked tawny, rest of wing-coverts greyish-brown, spotted blackish-brown, tawny, buff and pale buff; scapulars blackish-brown, broadly edged buff on outer webs; white band around throat; underparts greyish-brown speckled brown and spotted buff, becoming buff barred brown on belly and flanks. Both sexes have white spot on second, third and fourth outermost primaries and white

tips to two outermost tail feathers. Iris dark brown, bill blackish, legs and feet blackish. *C. macrurus* is larger and more variegated; male has larger white wing spots and broader, whiter tips to two outermost tail feathers, female having buff wing and tail markings. *C. celebensis* tends to show whiter tips to two outermost tail feathers. Immature similar to adult but browner and paler. Voice. Song of male is a repetitive "took-toor-r-r" given from perches, mainly at dusk and dawn.

Habitat. Typically primary and secondary forest, pine forest and second growth; also scrubland, open country with clumps of trees, mangroves, town and village outskirts, agricultural areas and by rocky beaches. Recorded from sea-level to 2000 m.

Food and Feeding. Probably feeds on insects. Foraging methods not documented.

Breeding. Poorly known. Breeds Apr-May, possibly longer, throughout range. No nest, eggs laid on leaf litter on ground, usually in forest or woodland clearing, or beside track or path. Clutch 1-2 eggs, elliptical or ovate, whitish, heavily blotched and spotted brown, dark brown and grey; chick semi-precocial, covered in brownish-rufous down.

Movements. None documented. Sedentary.

Status and Conservation. Not globally threatened. Widespread but probably not common anywhere throughout its range. Fairly common in Angat forest, near Manila, Luzon. Occurs in Rajah Sikatuna National Park (Bohol) and Mount Katanglad National Park (Mindanao).

Bibliography. Brooks, Dutson *et al.* (1996), Brooks, Evans *et al.* (1992), Danielsen *et al.* (1994), Delacour & Mayr (1946), Dickinson *et al.* (1991), Evans, Dutson & Brooks (1993), Inskipp *et al.* (1996), Marshall (1978), McGregor (1904, 1905), Mees (1977a, 1985b), Ogilvie-Grant (1894), Rabor (1977), Rand & Rabor (1960).

61. Sulawesi Nightjar *Caprimulgus celebensis*

French: Engoulevent des Célèbes

Spanish: Chotacabras de Célebes

German: Sulawesinachtschwalbe

Taxonomy. *Caprimulgus celebensis* Ogilvie-Grant, 1894, Sulawesi.

Forms superspecies with *C. macrurus*, *C. atripennis* and *C. manillensis*, and all four were formerly considered conspecific; in recent years has commonly been lumped in *C. manillensis*, but differs in both voice and morphology. Two subspecies recognized.

Subspecies and Distribution.

C. c. celebensis Ogilvie-Grant, 1894 - N & CE Sulawesi; probably also Buton I in SE.

C. c. jungei Neumann, 1939 - Sula Is, where currently known from Taliabu and Mangole.



Descriptive notes. 24-30 cm. Sexes similar. Upperparts greyish-brown streaked blackish-brown, broadly so on central crown, with no nuchal collar; lesser coverts dark brown speckled tawny and buff, rest of wing-coverts greyish-brown, boldly spotted buff, pale buff and tawny; scapulars blackish-brown edged buffish; white throat patch; underparts greyish-brown, speckled and spotted brown, greyish-white and buff, becoming buff barred brown on belly and flanks. Both sexes have white spot on second, third and fourth outermost primaries and white tips to two outermost tail feathers. Iris dark brown, bill blackish, legs and feet blackish. Differs from *C. manillensis* by whiter tips to two outermost tail feathers. Smaller and plainer than *C. macrurus*, with smaller white wing spots and narrower white tips to two outermost tail feathers in male. Paler and less spotted than *Eurostopodus diabolicus*, which has broad band around throat, smaller white wing spots and no white on tail. Race *jungei* has smaller white tips to two outermost tail feathers. Voice. Song of male is an accelerating "tok, tok, tok, tr, tr, tr", last notes softer and trailing off; sings from perches, mainly at dusk.

Habitat. Typically, secondary forest, coastal bush and edges of mangroves. On Taliabu, lowland forest, including lightly logged areas.

Food and Feeding. Poorly documented. Probably feeds on insects. Forages by hawking after prey in buoyant and agile flight.

Breeding. Breeding habits not documented.

Movements. None documented. Probably sedentary.

Status and Conservation. Not globally threatened. Restricted-range species; present in Sulawesi EBA and Banggai and Sula Islands EBA. Locally rare to fairly common in parts of N & E Sulawesi, but clearly under-recorded; only recently discovered on Buton I, where status uncertain; in Sula Is. reasonably common on Taliabu and uncommon on Mangole. Present in Tangkoko Nature Reserve (NE Sulawesi). Loss of habitat due to deforestation probably most serious threat throughout its range. **Bibliography.** Andrew (1992, 1993), Catterall (1997), Coates & Bishop (1997), Davidson *et al.* (1995), Holmes & Phillips (1996), Inskipp *et al.* (1996), Mees (1977a, 1985b), Rozendaal (1990), Stones, Lucking *et al.* (1997), Watling (1983), White & Bruce (1986).

62. Donaldson-Smith's Nightjar

Caprimulgus donaldsoni

French: Engoulevent des épines

Spanish: Chotacabras Espinero

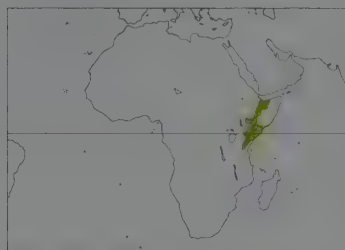
German: Dornbusch-Nachtschwalbe

Taxonomy. *Caprimulgus donaldsoni* Sharpe, 1895, Hargeysa, Somalia.

Monotypic.

Distribution. NW Somalia to NE Tanzania; possibly also SE Sudan.

Descriptive notes. 18 cm; male 21–36 g, female 26–36 g. Sexually dimorphic, but only slightly so. Upperparts greyish streaked brown; wing-coverts chestnut or rufous, streaked brown and spotted buffish; broad rufous, tawny and buff nuchal collar; underparts chestnut or rufous, heavily spotted buff, becoming dark buff barred brown on belly. Male has white spot on four outermost primaries and broad white tips to two outermost tail feathers; female has smaller white markings. Iris, bill, legs and feet all dark brown. Some variation in general coloration, and greyer or browner birds occur. Immature similar to adult female but rather rufous. **VOICE.** Song of male is a series of melodious whistles, “tu-wee, tu”, given from ground mainly at dusk and dawn.



Habitat. Mainly arid or semi-arid scrubland and bush country, also wooded wadis, from sea-level to 1700 m.

Food and Feeding. Diet includes ants, grasshoppers, moths, beetles and caterpillars. Forages by hawking after prey, often close to ground or over water. When hunting, flight is extremely rapid and agile. Occasionally takes food from ground.

Breeding. Poorly documented. Breeds May–Jun in Somalia, and possibly Aug–Oct in Kenya. No nest, eggs laid usually on sandy ground, generally beneath vegetation such as small bush. Clutch 2 eggs, ovate, dullish ivory,

heavily marbled greyish-brown on patches of violet-grey; chick not described.

Movements. Poorly understood and possibly sedentary in parts of its range; common in Ilemi Triangle (S Sudan) in Feb and Jun, but apparently absent Nov–Dec and occurrence there possibly seasonal only.

Status and Conservation. Not globally threatened. Widespread and locally common to abundant up to 1400 m throughout range, less common at higher altitudes. Seasonally common in suitable habitat in SE Sudan, where may not breed; locally uncommon to common in Kenya and N Tanzania. Present in Tsavo West, Tsavo East and Awash National Parks (Kenya).

Bibliography. Archer & Godman (1937–1961), Ash & Miskell (1983b, 1998), Britton (1980), Brown & Britton (1980), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Duckworth *et al.* (1992), Fry *et al.* (1988), Lack & Quicke (1978), Lewis & Pomeroy (1989), Mackworth-Praed & Grant (1957), Nikolaus (1987, 1989), Short *et al.* (1990), Snow (1978), Tilahun *et al.* (1996), Urban & Brown (1971), Zimmerman, D.A. *et al.* (1996).



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ssp pectoralis

ssp fervidus

normal morph

ssp ruwenzorii

ssp guttifer

grey bird

rufous bird

PLATE 33

inches 5
cm 13

63. Black-shouldered Nightjar

Caprimulgus nigriscapularis

French: Engoulevent à épaulettes noires

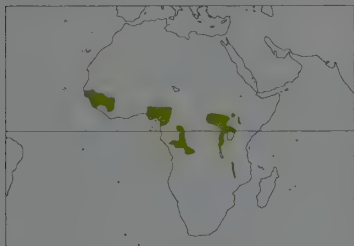
Spanish: Chotacabras Hombro Negro

German: Schwarzschilder-Nachtschwalbe

Other common names: Dusky Nightjar(!)

Taxonomy. *Caprimulgus nigriscapularis* Reichenow, 1893, Songa, west of Lake Albert. Often considered conspecific with *C. pectoralis*; these two form superspecies with *C. poliocephalus* and *C. ruwenzorii*. Monotypic.

Distribution. Patchily from Gambia, Senegal and W Sierra Leone E through Nigeria and Cameroon to SE Sudan and W Kenya, and S to Congo and SW Zaire.



Descriptive notes. 23-25 cm; male 48-50 g. Sexually dimorphic. Upperparts generally dark brown tinged rufous; broad tawny-buff nuchal collar; lesser coverts blackish-brown, rest of wing-coverts brown spotted buffish; scapulars blackish-brown edged buff; white throat patch; underparts rufescent-brown, becoming tawny-buff on belly and flanks. Male has small white spot on four outermost primaries and broad white tips to two outermost tail feathers; female has slightly smaller white markings. Iris dark brown, bill blackish, legs and feet dark brown. More rufous than *C. pectoralis*, with more strikingly patterned wing-coverts, rufous

nuchal collar and smaller white wing spots. Paler and more rufous than *C. poliocephalus* and *C. ruwenzorii*, with less white on two outer tail feathers. Immature similar to adult but more rufous. **VOICE.** Song of male is an evenly pitched, double-noted whistle, "pee-u-o, piririri" or "pee-u-o, pererere", second note being trilled, often preceded by a rapid series of "werp" notes. Sings from perches at dusk and dawn and on moonlit nights. Calls include soft "chuk", "tuc" and double "tuc-tuc" sounds.

Habitat. Favours mainly edges of lowland forest: dense woodland, gallery forest, rainforest, secondary growth, and sparsely wooded, grassy or stony hillsides. In W Kenya, also mossy thickets with small trees. Recorded from sea-level to c. 2000 m.

Food and Feeding. Poorly studied. Feeds on moths, beetles and other insects. Forages by hawking for prey among trees, in clearings, over open areas or above hillsides.

Breeding. Breeds possibly May in Gambia, Aug-Dec (chicks found Sept and Dec) in W Zaire, Apr-Aug in N Zaire, Jan-Feb in NE Zaire, Feb-Jun and Sept-Dec in Uganda, and Jul-Mar (singing males) in S Nigeria. No nest, eggs laid on ground, usually on leaf litter, often in woodland clearing. Clutch 1-2 eggs, elliptical, pale or creamy pink, speckled reddish-brown and grey, markings usually concentrated in band around blunt end; incubation period not documented; chick semi-precocial, covered in pale greyish-buff down, fledging period unknown; adults threatened at nest-site may perform injury-feigning distraction display.

Movements. None documented. Possibly sedentary.

Status and Conservation. Not globally threatened. Frequent to common in many parts of range, and probably more common and widespread than currently documented. Few records W Senegal, W Gambia, Guinea Bissau and W Sierra Leone; possibly locally common in Ivory Coast, e.g. Comoé National Park; possibly not common in Ghana; rare in Togo; fairly common in forest zone in S Nigeria; possibly not uncommon in W Cameroon; locally common in E Zaire; not uncommon locally in W & S Uganda; locally common in Rwanda and Burundi, occurring in Ruwuvu National Park; local and uncommon in W Kenya; fairly common in extreme S Sudan.

Bibliography. Bannerman (1953), Barlow *et al.* (1997), Benson & Colebrook-Robjent (1977), Britton (1980), Cave & Macdonald (1955), Cheke & Walsh (1996), Cleere (1995a), Davis (1979a), Demey & Fishpool (1991), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Elgood *et al.* (1994), Field (1998), Fry (1988a), Fry *et al.* (1988), Gatter (1990), Grimes (1987), Lewis & Pomeroy (1989), Louette (1981, 1990b), Mackworth-Præd & Grant (1957, 1970), Morel & Morel (1990), Nikolaus (1987, 1989), Pérez del Val *et al.* (1997), Pinto (1983), Salewski (1997), Short *et al.* (1990), Snow (1978), Zimmerman, D.A. *et al.* (1996).

64. Fiery-necked Nightjar

Caprimulgus pectoralis

French: Engoulevent musicien

German: Pfeifnachtschwalbe

Spanish: Chotacabras Músico

Other common names: African Dusky Nightjar

Taxonomy. *Caprimulgus pectoralis* Cuvier, 1817, Knysna, Cape Province.

Often considered conspecific with *C. nigriscapularis*; these two form superspecies with *C. poliocephalus* and *C. ruwenzorii*. The three more northerly races have been considered so distinct from nominate that they may represent an incipient species (*C. fervidus*). Four subspecies currently recognized.

Subspecies and Distribution.

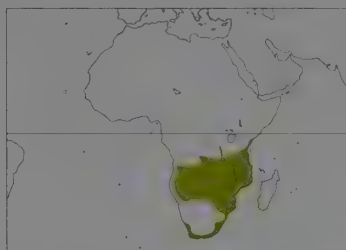
C. p. shelleyi Bocage, 1879 - Angola and S Zaire E to Tanzania and SE Kenya.

C. p. fervidus Sharpe, 1875 - S Angola, N Namibia, N & E Botswana and Zimbabwe to NE South Africa.

C. p. crepusculans Clancey, 1994 - S Malawi (possibly), SE Zimbabwe and Mozambique to E South Africa and E Swaziland.

C. p. pectoralis Cuvier, 1817 - S South Africa.

Descriptive notes. 23-25 cm; male 41-66 g, female 38-66 g. Sexually dimorphic. Upperparts dark brown, variegated greyish-brown and brownish-white, showing two or three rows of pale spots across wing-coverts; broad buff or tawny-buff nuchal collar; white submoustachial stripe and large white throat patch; underparts brown, speckled and barred brownish-white and buff. Male has large white spot on four outermost primaries and broad white tips to two outermost tail feathers; female has smaller, buffier white markings. Iris brown, bill blackish, legs and feet brown. Generally greyer and browner than *C. nigriscapularis*, especially on underparts, with buffier nuchal collar, paler lesser coverts and larger white wing spots. Paler and greyer than *C. poliocephalus* and *C. ruwenzorii*, with less white on two outermost tail feathers. Immature similar to adult but often paler and more



rufous. Races vary in overall coloration, in extent and coloration of nuchal collar, and in amount of barring on underparts; *fervidus* has a distinctive rufous morph, and this may also be present in other races. **VOICE.** Song of male is a melodious but variable whistle, "pee-u-o, piririri", first note undulating, second an evenly pitched trill, often preceded by a series of "werp" notes. Sings from perches, mainly at dusk and dawn and on moonlit nights. Alarm calls include "woot, woot, woot" notes and soft "chuk"; chirrs and guttural hissing sounds are given during distraction, threat or defence displays.

Habitat. Typically *Brachystegia* woodland savanna (miombo), but also commonly mopane and other deciduous woodland; in addition, occurs in scrubland, eucalyptus plantations, riparian forest, thickets and suburban gardens. Avoids thick forest interior but frequents forest edge. Recorded from sea-level to 1500 m.

Food and Feeding. Diet includes mantises, spiders, moths, grasshoppers and beetles. Forages by making flycatching sallies from perches. Also hawks for prey in flight and often feeds on insects disturbed or attracted by grazing animals. Drinks in flight.

Breeding. Breeds Aug-Sept in Angola, Sept-Nov in Zambia and Malawi, from Sept generally in E Africa, Aug-Dec in Botswana and Zimbabwe, and Aug-Nov in South Africa; in all areas periods possibly longer than given, and usually begin towards start of rains. Double-brooded, second clutch may be started 33 days after first hatches. Monogamous and territorial; territory up to 5-8 ha. Nest-site usually beneath tree within woodland, copse or wooded tract, also in thicket or acacia stand, tends to avoid arable land; no nest, eggs laid on leaf litter on ground. Clutch 1-2 eggs, usually 2, elliptical, glossy ivory-white to pale or creamy pink, plain or spotted and blotched reddish-brown, grey and dark pink, laid on successive days; incubation begins as soon as first egg laid, usually by female during day, period c. 18 days, eggs usually hatching asynchronously but on one occasion synchronously at night; replacement often laid if clutch lost; adults threatened at nest-site may perform injury-feigning distraction display; chick semi-precocial, covered with brown and grey down, fledges at c. 18 days but can remain dependent for further 24 days; young may stay in breeding area for up to 62-145 days.

Movements. Nominate race sedentary and partially migratory. At end of breeding season, moves N and NE (Apr-May) as far as SE Zimbabwe; one record from Barotse Province, Zambia, in Jul. Return movements to breeding grounds begin about early Sept. Race *shelleyi* sedentary and possibly partially migratory. Movements poorly understood, but at end of breeding season possibly moves S to N Namibia, N Botswana and NW Zimbabwe. Race *fervidus* migratory. Movements again poorly understood, but after breeding season probably moves N to N Zambia, SE Zaire and Tanzania. There are also possible records from Rwanda and Burundi. Race *crepusculans* possibly mainly sedentary.

Status and Conservation. Not globally threatened. Widely distributed and generally quite common throughout most of range. Few data published on population densities, though widespread and locally common in Zimbabwe, e.g. up to 20 pairs in 65 ha; locally common in coastal woodlands and forests of SE Kenya, e.g. common in Sokoke; locally common in S Zaire; widespread and common in Zambia; common in Malawi, occurring in Liwonde National Park; fairly common to very common in Botswana, where occurs in Chobe National Park; fairly common in N Namibia; locally common in NE South Africa, e.g. in Kruger National Park. Nominate race locally very common, e.g. in Bontebok Nature Reserve.

Bibliography. Aspinwall (1982), Benson & Benson (1977), Benson & Colebrook-Robjent (1977), Benson *et al.* (1971), Britton (1980), Britton & Britton (1973), Cave & Macdonald (1955), Chenuaux-Repond (1980), Clancey (1994, 1996), Cleere (1995a), Colebrook-Robjent (1979, 1984), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Fry (1988a), Fry *et al.* (1988), Ginn *et al.* (1989), Gore (1990), Harrison *et al.* (1997), Harwin (1982), Hockey *et al.* (1989), Jackson (1975, 1978, 1983, 1984a, 1984b, 1985a, 1985c, 1986, 1987), Langley (1984), Lewis & Pomeroy (1989), Lippens & Wille (1976), Louette (1990b), Mackworth-Præd & Grant (1957, 1962, 1970), Maclean (1993), Masterson (1994), Penry (1994), Pinto (1983), Short *et al.* (1990), Snow (1978), Steyn (1996a, 1996b), Steyn & Myburgh (1975), Vernon & Dean (1988), Zimmerman, D.A. *et al.* (1996).

65. Abyssinian Nightjar

Caprimulgus poliocephalus

French: Engoulevent d'Abyssinie

Spanish: Chotacabras Abisinio

German: Höhnennachtschwalbe

Other common names: Montane Nightjar(!), Mountain Nightjar

Taxonomy. *Caprimulgus poliocephalus* Rüppell, 1840, Kulla, Ethiopia.

Often considered conspecific with *C. ruwenzorii*; these two form superspecies with *C. nigriscapularis* and *C. pectoralis*. Population in Saudi Arabia possibly racially distinct, requires further study. Race *guttifer* and proposed race *koesteri* of *C. ruwenzorii* have sometimes been placed in present species. Monotypic.

Distribution. SW Saudi Arabia and possibly Yemen, discontinuously through C Ethiopia to NE Uganda and N Tanzania.



Descriptive notes. 22-24 cm; male 42-50 g, female 42-50 g. Sexually dimorphic. Upperparts greyish-brown streaked blackish-brown, broadly so on central crown; broad buff or tawny-buff nuchal collar; wing-coverts are greyish-brown, speckled greyish-white and spotted pale buff; scapulars blackish-brown, broadly edged buff; whitish submoustachial stripe and white throat patch; underparts are greyish-brown, speckled and spotted buff, greyish-white and cinnamon, becoming buff barred brown on belly and flanks. Male has white spot on four outermost primaries, and two outermost tail feathers are generally

white; female has smaller white wing spots, edged or washed buff, and less white in tail. Iris dark brown, bill blackish, legs and feet darkish brown. Paler than *C. ruwenzorii*, with larger white wing spots and more white on outer tail feathers. Darker and browner than *C. pectoralis*, with more white in tail. Darker and browner than *C. nigriscapularis*, with larger white wing spots and more white in tail. Immature paler than adult and often rather rufous. Voice. Song of male is a double-noted whistle, "peuu-eee, pe-uu-uu", first note undulating, second note trilled and descending slightly in pitch. Sings from perches. Flight call is a series of deep "kah, kah, kah" notes.

Habitat. Mainly found in interior and at edges of all types of montane woodland and forest, including olive, pine, juniper and bamboo; also occurs in large wooded suburban gardens, steep rocky hillsides with scattered eucalyptus, and more open wooded areas. In Saudi Arabia, apparently prefers rocky terrain with juniper forest. Recorded at 1000-3350 m.

Food and Feeding. Feeds on moths, beetles and grasshoppers. Forages by hawking for prey in open spaces such as fields and pastures, open woodland and large suburban gardens with plenty of trees. When hunting, flight is extremely agile and rapid. Also flycatches from perches, flying with shallow wingbeats interspersed with many twists and turns. Also feeds on insects attracted to artificial lights and fires.

Breeding. Poorly documented. Breeds possibly Mar-May in Saudi Arabia, Feb-May in Ethiopia, and Sept-Jan in Sudan, Uganda, Kenya (also Mar-Apr) and N Tanzania. Monogamous and territorial. Nest-site usually in small clearing at or near base of tree or bush, in suburban garden, occasionally alone or within hedgerow; no nest, eggs laid on bare ground or leaf litter. Clutch normally 2 eggs, elliptical, creamy-pink to pinkish-buff, spotted and blotched pale brown or reddish-brown, markings heavier around blunt end; incubation mainly by female; chick not described.

Movements. None documented throughout African range and probably sedentary. In Saudi Arabia, may move to lower altitudes in winter.

Status and Conservation. Not globally threatened. Locally common throughout range. Widespread and locally common along W side of Asir Mts, SW Saudi Arabia, range possibly extending S into Yemen highlands. In Ethiopia, common in suitable forested highlands between 1800-3200 m in W, SE & Rift Valley, less common but frequent between 3200-3350 m; occurs in Bale Mountains National Park. Locally common between 1000-3000 m in SE Sudan, NE Uganda, highlands of W & C Kenya and N Tanzania.

Bibliography. Britton (1980), Brown & Britton (1980), Cave & Macdonald (1955), Cheesman & Selater (1935), Cleere (1995a), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Evans (1994), Fry (1988a), Fry *et al.* (1988), Jennings (1995), Lewis & Pomeroy (1989), Louette (1990b), Mackworth-Præd & Grant (1957), Newton (1992), Nikolaus (1987, 1989), Porter, Christensen & Schiermacker-Hansen (1996), Short *et al.* (1990), Snow (1978), Stagg (1992), Symens, Newton, Stagg & Winkler (1993), Symens, Newton, Winkler & Stagg (1992), Urban & Brown (1991), Wilson & Wilson (1994), Zimmerman, D.A. *et al.* (1996).

66. Montane Nightjar

Caprimulgus ruwenzorii

French: Engoulevent du Ruwenzori **Spanish:** Chotacabras del Ruwenzori
German: Ruwenzorinachtschwalbe
Other common names: Ruwenzori Nightjar

Taxonomy. *Caprimulgus ruwenzorii* Ogilvie-Grant, 1908, Mubuku Valley, Mt Ruwenzori. Often considered conspecific with *C. poliocephalus*; these two form superspecies with *C. nigriscapularis* and *C. pectoralis*. Angolan population has been separated as race *koesteri*, and in tail pattern appears intermediate between nominate and *guttifer*; this isolated population has even been suggested to be a separate species. Race *guttifer* has occasionally been treated as a separate species. Both of these forms have alternatively been considered races of *C. poliocephalus*. Two subspecies currently recognized.

Subspecies and Distribution.
C. r. ruwenzorii Ogilvie-Grant, 1908 - SW Uganda to E Zaire; separate population in W Angola.
C. r. guttifer Grote, 1921 - SW Tanzania, N Malawi and NE Zambia; separate population in NE Tanzania.



wing spots tinged buffish and less white on tail. Iris dark brown, bill blackish, legs and feet dark brown. Darker than *C. poliocephalus*, with smaller white wing spots and less white on two outermost tail feathers. Darker and browner than *C. pectoralis*, with smaller white wing spots and more white on tail. Darker and browner than *C. nigriscapularis*, with more white on tail. Immature similar to adult. Race *guttifer* has slightly less white on tail. Voice. Song of male is a double-noted whistle, "pee-eee, pee-uuu", first note evenly pitched, second slightly trilled. Sings from perches, mainly at dusk and dawn and on moonlit nights. Flight calls are soft "ka, ka, ka, kah" notes; other calls include soft "kweep" and "yip, yip" sounds.

Habitat. Typically, edges of all types of montane woodland and forest, including large tracts of introduced coniferous species, e.g. *Pinus patula*; also woodland clearings, open scrubland, small stands of woodland on montane grassland, bracken-covered ridges, bracken ferns and edges of bracken briers. Recorded at 1500-2800 m.

Food and Feeding. Feeds on moths, beetles and termites. Forages along edges of woods and forests, often among treetops, or over grasslands and other open areas. Also makes flycatching sallies from perches.

Breeding. Appears to be poorly documented. Breeds Aug/Sept-Mar throughout much of range, and Sept-Nov in N Malawi and NE Zambia. Nest-site in woodland clearing, burnt area, bracken brier, near rocks or boulders, on valley slope, or beneath tree, bush or sapling; no nest, eggs laid on bare ground. Clutch 1-2 eggs, elliptical, pale pinkish-cream to pale buff, speckled reddish-brown with markings denser around blunt end; chick not described.

Movements. None documented. Probably sedentary throughout whole of range.

Descriptive notes. 22-24 cm; male 43-55 g, female 41-57 g. Sexually dimorphic. Upperparts dark greyish-brown streaked blackish-brown, broadly so on central crown; broad buff or tawny-buff nuchal collar; wing-coverts dark greyish-brown, speckled greyish-white and spotted pale buff; scapulars blackish-brown, broadly edged buff; whitish submoustachial stripe and white throat patch; underparts dark greyish-brown, speckled and spotted buff and pale buff, becoming buff barred brown on belly and flanks. Male has small white spot on four outermost primaries, and two outermost tail feathers are white distally; female has white

Status and Conservation. Not globally threatened. If race *guttifer* and Angolan population are placed in *C. poliocephalus*, present species becomes restricted-range species: present in Albertine Rift Mountains EBA. Little known, but locally common in suitable habitat. Locally common in forested uplands from SW Uganda S through Rwanda, Burundi and E Zaire to SW Tanzania, N Malawi and NE Zambia; possibly also locally common in NE Tanzania and Angola. Occurs in Impenetrable Forest National Park (SW Uganda) and Kibira National Park (NW Burundi).

Bibliography. Benson & Benson (1977), Benson *et al.* (1971), Britton (1980), Chapin, J.P. (1939), Chapin, R.T. (1978), Chappuis (1981), Cleere (1995a), Colebrook-Robjent (1979), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Fry (1988a), Fry *et al.* (1988), Hall (1960), Johnston-Stewart & Heigham (1982), Lippens & Wille (1976), Louette (1990b), Mackworth-Præd & Grant (1957, 1962, 1970), Newman *et al.* (1992), Pinto (1983), Short *et al.* (1990), Snow (1978), Stattersfield *et al.* (1998), Symens *et al.* (1992), Turner *et al.* (1991), Zimmerman, D.A. *et al.* (1996).

67. Indian Nightjar

Caprimulgus asiaticus

French: Engoulevent indien **German:** Hindunachtschwalbe **Spanish:** Chotacabras Hindú
Other common names: (Southern) Common Indian Nightjar, Little Indian Nightjar

Taxonomy. *Caprimulgus asiaticus* Latham, 1790, Bombay.

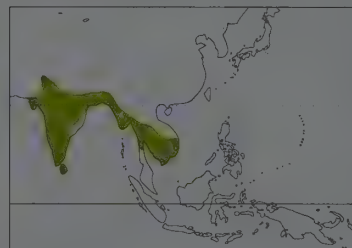
In past, sometimes considered conspecific with *C. madagascariensis*. Three subspecies recognized.

Subspecies and Distribution.

C. a. asiaticus Latham, 1790 - SE Pakistan and India to S Thailand and S Indochina.

C. a. eidos J. L. Peters, 1940 - Sri Lanka.

C. a. siamensis Meyer de Schauensee, 1934 - N Thailand.



Descriptive notes. 24 cm; 1 male 46 g. Sexually dimorphic. Upperparts greyish-brown streaked blackish-brown, crown broadly streaked blackish-brown edged rufous; broad buff or tawny nuchal collar; lesser coverts greyish-brown speckled rufous, rest of wing-coverts greyish-brown boldly spotted buff; scapulars blackish-brown edged buff; whitish submoustachial stripe and large white patch on either side of lower throat; underparts greyish-brown, barred brown and boldly spotted buff, becoming buff barred brown on belly and flanks. Male has white spot on four outermost primaries and broad white tips to two outer-

most tail feathers; female has smaller white wing spots, tinged or edged buff, and narrower buffish white tips to two outermost tail feathers. Iris dark brown, bill blackish, legs and feet brownish. Slightly smaller than *C. indicus*, with broader nuchal collar; male has smaller white wing spots and only two outermost tail feathers tipped white. Smaller than *C. macrurus*, with more distinct nuchal collar and more boldly spotted wing-coverts; male has smaller white wing spots and narrower white tips to two outermost tail feathers. Generally more heavily patterned than *C. affinis*, which usually lacks a nuchal collar and has less spotting on wing-coverts; male of that species often has larger white wing spots and two outermost tail feathers are entirely whitish. Juvenile paler and plainer than adult. Racial differences slight; nominate race variable in colour, with greyish-brown, sandy-buff, grey, brown and rufous birds recorded; race *eidos* possibly slightly smaller; race *siamensis* paler and more silvery-grey, with paler nuchal collar. Voice. Song of male is a distinctive "chuk-chuk-chuk-k-k-k-roo". Sings from perches and occasionally from ground, mainly at dusk and dawn and on moonlit nights. Flight calls are possibly short "quit-quit" or "chuk-chuk" notes.

Habitat. Highly variable throughout range, but typically scrubland or wooded country. Light scrub jungle, thin bamboo jungle, young forestry plantations, fallow cultivation with thickets and euphorbia hedges, stony nullahs near cultivation, and overgrown gardens. In SW Pakistan, prefers low hill country, sparsely vegetated with scattered thorn scrub, but also low stony hills and flat saline areas with tamarisk bushes. In Sri Lanka, scrubland, waste ground, tracts of jungle on sandy soils, open wooded country and cinnamon plantations. Lowland plains to foothills, from sea-level to 1500 m.

Food and Feeding. Diet includes moths, beetles, grasshoppers, crickets and bugs. During non-breeding season, also takes flowers of *Euphorbia caducifolia* and possibly small mice. Foraging behaviour not fully documented, but recorded feeding on insects attracted to artificial lights, and occasionally takes prey from ground.

Breeding. Surprisingly poorly documented. Breeds from Apr in Pakistan, Feb-Sept (mainly Apr to perhaps May) in India, Jan-Oct (mainly Mar-May and Sept) in Sri Lanka, and from mid-Mar in Thailand. Possibly double-brooded. Nest-site in open or shaded by vegetation, usually close to bush or tree stump, beneath tree or sapling, at base of man-made wall, in dry, pebbly nullah or in stony field; no nest, eggs laid on leaf litter or bare soil. Clutch 2 eggs, elliptical, cream or pale salmon-pink, spotted and smeared reddish-brown and purple; both sexes incubate, period not documented; chick covered in rufous down, fledging period not documented.

Movements. Poorly known. Nominally race possibly sedentary, and also partially and locally migratory, e.g. in S Pakistan, though movements often not fully understood. Other races appear to be sedentary.

Status and Conservation. Not globally threatened. Generally common and widespread throughout range. In S Pakistan, locally common in Thatta, Badin and Thar Park districts only; occurs in Khirtar National Park. In India, found in several protected areas, e.g. Keoladeo Ghana National Park. In Sri Lanka, common in suitable habitat in dry areas, less common in wet areas; very common in Yala National Park in dry SE of island; also occurs in Uda Walawe National Park. In Thailand, present in Khao Sam Roi Yot National Park.

Bibliography. Ali (1996), Ali & Ripley (1983), Barnes (1937), Bharos (1992), Chakravarthy & Purna Chandra Tejassvi (1992), Daniels (1997), Deignan (1945), Eames & Ericson (1996), Grinnett *et al.* (1998), Harvey (1989), Henry (1998), Hue & Fitchécar (1970), Inskipp & Inskipp (1991), Jones (1923), Lamba (1967), Legge (1983), Lekagul & Round (1991), Lowther (1937), Mahabadi & Lamba (1987), Majumdar *et al.* (1992), Marshall (1978), Mukherjee (1995), Osmaston (1921a), Parrot (1907), Phillips (1978), Porter, Christensen & Schiermacker-Hansen (1996), Rana (1988), Riley (1938), Ripley (1982), Roberts (1991), Round (1988), Smythies (1986), Stepanyan (1995), Whistler & Kinnear (1935).

68. Madagascar Nightjar

Caprimulgus madagascariensis

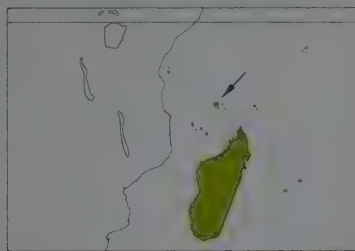
French: Engoulevent malgache **Spanish:** Chotacabras Malgache
German: Madagaskarnachtschwalbe

Taxonomy. *Caprimulgus Madagascariensis* Sganzin, 1840, Sainte Marie, Madagascar.
In past, sometimes considered conspecific with *C. asiaticus*. Racial differences uncertain, and species may be better considered monotypic. Two subspecies currently recognized.

Subspecies and Distribution.

C. m. aldabrensis Ridgway, 1894 - Aldabra.

C. m. madagascariensis Sganzin, 1840 - Madagascar (including Nosy Boraha).



Descriptive notes. 21-23 cm; male 37-43 g, female 45-51 g, unsexed 43-44 g. Sexually dimorphic. Upperparts greyish-brown streaked blackish-brown, generally no nuchal collar; lesser coverts greyish-brown speckled buffish and tawny, rest of wing-coverts greyish-brown, heavily spotted buff with brown centres; scapulars blackish-brown edged buff; whitish submoustachial stripe and small white patch on either side of lower throat; underparts greyish-brown thinly barred greyish-white, becoming buff barred brown on belly and flanks. Male has white spot on four outermost primaries and white tips to two outermost tail feathers; female has buff wing spots and smaller white tips to tail feathers. Iris dark brown, bill blackish, legs and feet dark brown. Paler and more variegated than *C. enarratus*, with no nuchal collar, small white wing spots, and much broader white tips to two outermost tail feathers. Immature similar to adult female. Race *aldabrensis* is occasionally paler on crown and scapulars, with broader white tips to two outermost tail feathers. VOICE. Song of male is a repetitive "tuk-tr-tr-tr-tr-tr"; occasionally gives "cop, cop, cop" notes, a soft cooing or a faint, wavering "huuu". Sings from perches or ground, throughout night. Calls include loud, liquid "wa-pit" or "tyo" and muffled "chok" sounds.

Habitat. All types of open or lightly wooded country: woodland, including partially or totally degraded areas, clearings, forest edges, savanna, heathland, scrubland, eucalyptus plantations, areas of afforestation; also in cultivated regions, near urban areas and in gardens. Tends to avoid dense forest. On Aldabra, open sandy hills, also casuarina woods with sparse understorey. Recorded from sea-level to 1800 m.

Food and Feeding. Feeds on grasshoppers, moths, cicadas and beetles. Forages by hawking around tree-tops, in open country or over water. When hunting, frequently glides with wings held above back. Usually forages alone, although large numbers may occur together where there is a plentiful food supply. On Aldabra, also hunts over sand dunes and around habitation.

Breeding. Breeds Aug to perhaps Oct in SW Madagascar, Oct-Nov in N Madagascar, and Sept-Dec on Aldabra. No nest, eggs laid usually on ground, often on leaf litter, and typically in open woodland or forest, or in clearing, apparently also on flat roof; on Aldabra, also on bare soil or gravel, often on open sandy hill, or beneath bush in clearing or alongside path in thick scrub. Clutch 2 eggs, elliptical, glossy white, blotched and spotted brownish-grey or blackish-grey; incubation probably by female during day, period not documented; adults threatened at nest-site perform defence display; chick semi-precocial, covered in brown and buff down, fledging period not documented.

Movements. None documented. Probably sedentary.

Status and Conservation. Not globally threatened. Common and widespread throughout Madagascar, especially in E; in some regions in SE, vocalizations suggest densities of up to 6 birds per 0.5 km²; occurs in Ranomafana National Park, Berenty Reserve and Perinet Special Reserve. Not uncommon on Aldabra Atoll, where population of several hundred individuals may be present, occurring on most islands, including terrestrial areas as small as 400 m². In Madagascar, environmental damage does not appear to pose immediate threat, as species apparently adaptable and tolerant of disturbed habitats; on Aldabra, natural predators may have included Common Barn-owl (*Tyto alba*) in past, though that species now considered extinct there; introduced threats may include rats and domestic and feral cats.

Bibliography. Appert (1996), Benson (1967b), Benson & Penny (1971), Benson *et al.* (1976-1977), Collin & Collin (1996), Dee (1986), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Goodman & Parrillo (1997), Goodman *et al.* (1997), Langrand (1995), Milon *et al.* (1973), Morris & Hawkins (1998), Mustoe *et al.* (1998), Penny (1974), Rand (1936), Safford & Duckworth (1990), Skerrett (1996), Young (1995).

69. Swamp Nightjar

Caprimulgus natalensis

French: Engoulevent du Natal **German:** Natalnachtschwalbe **Spanish:** Chotacabras del Natal
Other common names: African White-tailed Nightjar, Natal Nightjar

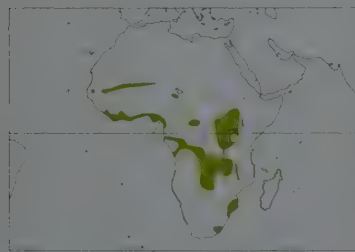
Taxonomy. *Caprimulgus natalensis* A. Smith, 1845, Durban.

Nominate incorporates possible races: *chadensis* (Sahel zone S to W Uganda); *gabonensis* (WC Africa); *fulviventris* (Angola); *curpi* (Caprivi Strip, Namibia); and *mpusa* (Zambia). Two subspecies currently recognized.

Subspecies and Distribution.

C. n. natalensis A. Smith, 1845 - very patchily from E Gambia to SW Ethiopia and S to E South Africa.

C. n. accrae Shelley, 1875 - coastal strip from NC Sierra Leone to W Cameroon.



Descriptive notes. 20-24 cm; 1 male 86.5 g, 1 female 65 g. Sexually dimorphic. Upperparts brown or greyish-brown, heavily spotted with large, irregularly shaped dark brown marks on wing-coverts, scapulars and tertials; indistinct pale buff or buff nuchal collar; white throat patch; underparts brown, heavily spotted buff or buffish-white, becoming buff barred brown on belly. Male has large white spot on four outermost primaries, and two outermost tail feathers extensively white; female has buffish or pale tawny wing spots and narrow buffish-white tips to tail feathers. Iris brown, bill dark brown, legs and feet pinkish-brown. Variable in coloration.

commonest forms being brown, greyish-brown or buffish-brown. Immature similar to adult but more spotted on upperparts. Race *accrae* darker, plainer and smaller. VOICE. Song of male is a monotonous "chop, chop, chop, chop" given from ground. Flight call is a rapid "chip, chip, chip, chip", courtship calls given by both sexes are "whip, whip, whip" or melodious "wip, lulululul" notes; other calls include soft "crup" and low "kik" notes.

Habitat. Mainly wet or damp habitats, sparsely vegetated with tufts or clumps of grasses, plants and other vegetation: grassland, meadows, swamps, marshes, bogs and dambos, marshy floodplains and vleis, and lagoon edges. Also along edges of woods and forest and in drier *Echinochloa* grassland. In W Africa, also damp grassy clearings in forest; in South Africa, frequently in areas with palms. Burnt habitats unsuitable, tends to vacate areas after fires. Recorded from sea-level to 2200 m.

Food and Feeding. Diet includes moths, termites, bugs and beetles. Foraging methods poorly documented, but recorded hunting around termite hills, pastures and cattle pens, often flying low over ground.

Breeding. Breeds from Mar in Sierra Leone, Apr-May in Nigeria, possibly mid-Aug to Oct in SE Gabon, Apr-Jun in W Kenya, Mar-May in NE Zaire, Aug-May in S Zaire, Jan-Mar, Jun-Aug and Oct in C & S Uganda, Sept-Nov in Zambia, and Aug-Nov in Angola, NW Zimbabwe and Natal. Monogamous. Nest-site often in long grass at edge of marsh or airstrip, or on sandy riverbank; no nest, eggs laid on bare soil, usually close to grass. Clutch usually 2 eggs, elliptical, slightly glossy, whitish, pinkish or pale grey with faint lilac patches and indistinctly spotted grey and speckled brown; both sexes incubate, female by day and male by night, period not more than 20 days (at one nest in Zimbabwe); chick covered in whitish down, dark grey on rump, though at Zimbabwe nest the chicks had dark grey/brown down; fledging period not documented.

Movements. Poorly known. Both races probably sedentary throughout much of range, although local movements may be triggered by loss of habitat, e.g. flooding after rains, or fire.

Status and Conservation. Not globally threatened. Rare in Gambia, though status uncertain; uncommon in Sierra Leone; widespread but mainly in coastal regions in Liberia; locally uncommon on Acra plains in Ghana; fairly common locally in Nigeria; rare on shores of L Chad but common in C Sudan (Nile Sudd), widely distributed but local in S. Locally common in N Congo, e.g. 4-5 pairs/km² in Odzala National Park; widespread and locally common in NE & S Zaire; fairly widespread and locally common in Uganda; uncommon to common locally in W Kenya; locally common between 600-2200 m in NW Tanzania; widespread and locally uncommon to frequent in N & W Zambia; locally common in region of Kazungula and upper Zambezi in Zimbabwe, with concentrations of up to 50 pairs in suitable habitat; locally fairly common in N Botswana; formerly widespread in Natal, South Africa, now locally uncommon to common; listed as vulnerable in South African Red Data Book. Throughout wide range, occurs in many protected areas, e.g. Ruwenzori National Park (Uganda), Ruvuvu National Park (Burundi) and Mkuzi Game Reserve (South Africa). Possibly locally common in suitable habitat throughout other parts of range. Major threats appear to be loss of habitat as a result of drainage, cultivation or fires, and damage from grazing and trampling by large herbivores. In Zimbabwe, effects of grassland burning unclear: might be favourable or detrimental to grass species required by present species; significance of different timing of burning could usefully be studied.

Bibliography. Anon. (1996b), Bannerman (1953), Barlow *et al.* (1997), Benson *et al.* (1971), Britton (1980), Brooke (1984), Cave & Macdonald (1955), Chapin (1939), Christy & Clarke (1994), Clancey (1996), Colebrook-Robjent (1979), Dowsett (1989a), Dowsett & Dowsett-Lemaire (1993, 1997), Dowsett & Forbes-Watson (1993), Elgood *et al.* (1994), Evans & Balmford (1992), Field (1998), Fry *et al.* (1988), Gatter (1997), Ginn *et al.* (1989), Grimes (1987), Harrison *et al.* (1997), Harwin (1983), Hustler (1997), Hustler & Carson (1996), Hustler & Mitchell (1997), Jackson (1986, 1987), Lewis & Pomeroy (1989), Lippens & Wille (1976), Louette (1981, 1990b), Mackworth-Præd & Grant (1957, 1962, 1970), Maclean (1993), Nikolaus (1987, 1989), Penry (1994), Pinto (1983), Rand (1951b), Randall (1988), Short *et al.* (1990), Snow (1978), Steyn (1996a), Zimmerman, D.A. (1972), Zimmerman, D.A. *et al.* (1996).

70. Plain Nightjar

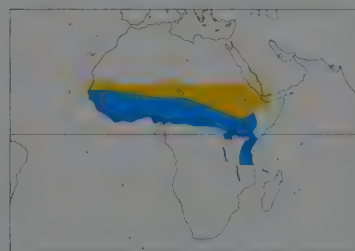
Caprimulgus inornatus

French: Engoulevent terne **German:** Marmornachtschwalbe **Spanish:** Chotacabras Sencillo
Other common names: Ludovic's Nightjar (possible race *ludovicianus*)

Taxonomy. *Caprimulgus inornatus* Heuglin, 1869, Bogosland.

Possibly forms superspecies with *C. stellatus*. Birds from SW Ethiopia formerly separated as race *ludovicianus*, which was sometimes considered a separate species. Birds of Niger formerly separated as race *vinaceobrunneus*. Monotypic.

Distribution. S Mauritania and N Senegal E to Ethiopia, NW Somalia and NW Kenya, and SW Saudi Arabia S into Yemen. Winters from Senegal and Liberia to SW Sudan and possibly SW Ethiopia, and S to Tanzania.



Descriptive notes. 22-23 cm; male 33-61 g, female 32-57 g. Sexually dimorphic. Upperparts and wing-coverts very variable in colour, blackish-brown, brown, greyish-brown, vinaceous, rufous, pale tawny-buff or sandy-buff, rather plain, with blackish-brown streaking and spotting on head and scapulars, and wing-coverts occasionally spotted buffish; no nuchal collar; lacks obvious white throat patch; underparts brownish or buff, barred brown. Male has white spot on four outermost primaries and broad white tips to two outermost tail feathers; female has tawny wing spots and lacks white in tail. Iris dark brown, bill brown with black tip, legs and feet pale brown. Has somewhat longer tail than *C. stellatus* and lacks white throat patch; broader white tips to two outermost tail feathers. Immature similar to adult. VOICE. Song of male is a prolonged, evenly pitched churr, occasionally beginning with a long series of deep cuck notes. Possibly sings from ground. Gives soft chuckles in flight; calls include low "chuk" notes. Makes guttural hissing sounds during threat or defence displays.

Habitat. Mainly savanna with trees and bushes, semi-desert steppes, less dense areas in lush savanna woodland, and grassy forest clearings. Outside breeding season, mainly wooded savanna. In Saudi Arabia, typically barren lowlands inland of Asir Mts, but also rocky terrain at higher altitudes. In Yemen, juniper forest on Jabal Iraf and in Wadi Hadramawt region, also slopes of arid wadis. Recorded from sea-level to 1800 m.

Food and Feeding. Poorly documented. Diet includes moths, termites, ants, grasshoppers, antlions, crickets, mantises and beetles. Forages by making flycatching sallies from ground or by hawking for prey in prolonged, buoyant flights.

Breeding. Poorly known. Breeds Apr-Jun in Mali, May-Jun in Niger, Mar-Jun in Ethiopia, Dec to mid-Jun in Somalia, May-Aug in NW Kenya (though nesting Mt Elgon in Sept) and Mar-May in Nigeria; possibly May-Jun in Liberia, where occasionally breeds (though two juveniles Dec and Jan); no data from Saudi Arabia or Yemen. Possibly monogamous. No nest, eggs laid on bare soil, usually near or under small bush. Clutch usually 2 eggs, elliptical-ovate, glossy ivory-white or creamy, spotted and speckled red-brown and lilac; incubation period not documented; chick covered with pale buff down, fledging period not known.

Movements. In Middle East, possibly a breeding summer visitor only in SW Saudi Arabia and Yemen; vagrant recorded off Kuria Muria Is, near Oman coast. In Africa, a breeding visitor (Apr-Nov) to Sahelian savannas. After breeding, moves S into wooded savannas along edges of rain-forest zone, occasionally straying into forests. Winters from Senegal to Liberia, E to NE Zaire, SW Sudan and possibly SW Ethiopia, S through Uganda, Kenya and N Tanzania to SC & E Tanzania. Passage migrants common N Nigeria (May-Jun and Nov-Dec) and regular N & E Kenya (Oct-Dec and Mar-Apr). Occasionally breeds within wintering range (Enugu, Nigeria; Mt Nimba, Liberia; Mt Elgon, Kenya) and possibly resident at Lagos, Nigeria. Vagrants recorded Gabon (Feb and Jul).

Status and Conservation. Not globally threatened. In Saudi Arabia, thought to be a summer visitor in small numbers but possibly under-recorded; locally common in Yemen. Generally rather common throughout much of African range: common in S Mauritania; uncommon, possibly seasonal visitor, in Senegal and Gambia but perhaps under-recorded; possibly not uncommon from Mali eastwards; locally uncommon in Ethiopia; common in Eritrea; fairly common in NW Somalia; uncommon seasonal migrant in Ghana but fairly common in Togo; in Nigeria, possibly resident in S but elsewhere fairly common migrant during dry season only; common seasonal visitor in NE Zaire; fairly widespread and seasonally common, though generally considered fairly uncommon, in W, C & S Kenya. Occurs in a number of protected areas, e.g. W National Park (SW Niger), Kabalega Falls National Park (W Uganda), and Tsavo West and Tsavo East National Parks (Kenya).

Bibliography. Ash & Miskell (1983b, 1998), Bannerman (1953), Barlow *et al.* (1997), Britton (1980), Brooks *et al.* (1987), Brouwer (1992), Cave & Macdonald (1955), Chapin (1939), Cheke & Walsh (1996), Christy (1984), Colston & Curry-Lindahl (1986), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Dymond (1996a), Elgood, Fry & Dowsett (1973), Elgood, Heigham *et al.* (1994), Evans (1994), Field (1998), Fry (1985), Fry *et al.* (1988), Gatter (1997), Gee (1984), Giraudoux *et al.* (1988), Grant & Mackworth-Praed (1946), Grimes (1987), Hollom *et al.* (1988), Jennings (1995), Lewis & Pomeroy (1989), Lippens & Wille (1976), Louette (1981, 1990b), Mackworth-Praed & Grant (1957, 1970), Nikolaus (1987), Porter & Martins (1993), Porter, Christensen & Schiermacker-Hansen (1996), Porter, Martins *et al.* (1996), Rand (1951b), Short *et al.* (1990), Snow (1978), Symens *et al.* (1992), Urban & Brown (1971), Zimmerman, D.A. *et al.* (1996).

71. Star-spotted Nightjar

Caprimulgus stellatus

French: Engoulevent étoilé **German:** Sternnachtschwalbe **Spanish:** Chotacabras Estrellado

Taxonomy. *Caprimulgus stellatus* Blundell and Lovat, 1899, Kassim River, southern Ethiopia.

Possibly forms superspecies with *C. inornatus*. Birds from lake region of S Ethiopia formerly separated as race *simplex*. Monotypic.

Distribution. NW Somalia, Djibouti, C & S Ethiopia, SE Sudan and NW, N & C Kenya.



Descriptive notes. 21-23 cm; male 54-64 g, female 50-69 g. Sexes similar. Slight colour variation noted with individuals ranging from greyish or vinaceous brown to paler, sandy brown. Upperparts and wing-coverts rather plain, generally dark greyish-brown, minutely speckled dark brown; crown and scapulars sparsely streaked and spotted dark brown, spots star-shaped; no nuchal collar; small white patch on either side of lower throat; underparts paler than upperparts, often brownish or buff barred brown. Both sexes have white spot on four outermost primaries and narrow white tips to two outermost tail feathers.

Iris dark brown, bill blackish, legs and feet flesh brown. Differs from more variable *C. inornatus* by white on throat and narrower white tips to two outermost tail feathers in male. Immature similar to adult but upperparts plainer and often rather rufous. **Voice.** Song of male is a soft, yelping "pweu, pweu, pweu, pweu" or "pwe-eh, pwe-eh, pwe-eh", given from ground, mainly at dusk and dawn. Flight call is possibly a guttural "churr-krk".

Habitat. Largely confined to dry, open bush and grassland, but also stony semi-deserts and black lava fields with densely scattered boulders, rocks and stones. Recorded from sea-level to possibly 1980 m.

Food and Feeding. Diet poorly studied. Feeds on moths, mantises, beetles and grasshoppers. Foraging methods not documented.

Breeding. Almost completely unknown. Possibly breeds Jan-Mar throughout range.

Movements. None documented. Sedentary.

Status and Conservation. Not globally threatened. Locally common in Ethiopia, especially in S, e.g. possibly one of commonest nightjars in Nechisar National Park; rare in SE Sudan; locally common in NW & N Kenya, where occurs in Marsabit Nature Reserve. Probably not very common throughout remainder of E African range, but probably under-recorded.

Bibliography. Ash & Miskell (1998), Britton (1980), Cave & Macdonald (1955), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Duckworth *et al.* (1992), Fry (1988a), Fry *et al.* (1988), Lewis & Pomeroy (1989), Mackworth-Praed & Grant (1957), Nikolaus (1987, 1989), Safford *et al.* (1993), Short *et al.* (1990), Snow (1978), Tilahun *et al.* (1996), Urban & Brown (1971), Zimmerman, D.A. *et al.* (1996).

PLATE 34

inches 4
cm 10



72. Savanna Nightjar

Caprimulgus affinis

French: Engoulevent affin **German:** Savannennachtschwalbe **Spanish:** Chotacabras de Sabana
Other common names: Allied Nightjar; Franklin's Nightjar (*monticolus* group)

Taxonomy. *Caprimulgus affinis* Horsfield, 1821, Java.

Races split into two distinct groups, formerly considered distinct species, but voice apparently identical: N populations, comprising first three races, form *monticolus* group; S populations, with remaining seven races, form *affinis* group. Birds from S Sulawesi may represent an undescribed taxon. Populations from NE India to Thailand formerly separated as race *burmanicus*. Ten subspecies currently recognized.

Subspecies and Distribution.

C. a. monticolus Franklin, 1831 - NE Pakistan and India E to Myanmar and S to Thailand, Cambodia and S Vietnam.

C. a. amoyensis Stuart Baker, 1931 - SE China and N Vietnam.

C. a. stictomus Swinhoe, 1863 - Taiwan.

C. a. griseatus Walden, 1875 - Luzon, Catanduanes, Mindoro, Sibuyan, Negros and Cebu (N Philippines).

C. a. mindanensis Mearns, 1905 - Mindanao (SE Philippines).

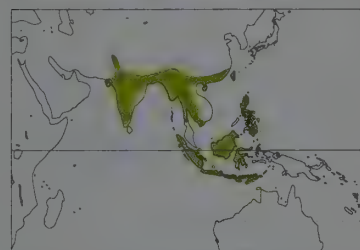
C. a. affinis Horsfield, 1821 - Sumatra, Borneo and Java, E to Lombok and possibly S Sulawesi.

C. a. propinquus Riley, 1918 - Sulawesi (possibly except Macassar region on S peninsula).

C. a. undulatus Mayr, 1944 - Sumbawa, Komodo and Flores (W Lesser Sundas).

C. a. kasudori Hachisuka, 1932 - Sawu and Sumba (C Lesser Sundas).

C. a. timorensis Mayr, 1944 - Alor, Timor, Roti and Kisar (E Lesser Sundas).



Descriptive notes. 20-26 cm; male 54-86 g, female 75-110 g. Sexually dimorphic. Upperparts brown, speckled whitish or cinnamon and streaked blackish-brown; pale buffish, cinnamon or whitish nuchal collar; lesser coverts brown speckled pale buff, rest of wing-coverts paler, boldly spotted pale buff; scapulars blackish-brown, broadly edged buff or whitish on outer webs; buffish submoustachial stripe and small white patch on either side of lower throat; underparts brown, barred, speckled and spotted buff and cinnamon, becoming buff barred brown on belly and flanks. Male has large white spot on four outermost primaries, and two outermost tail feathers are generally white, tipped or edged brownish; female has buffish wing spots and no white in tail. Iris dark brown, bill blackish, legs and feet brown. Less variegated than *C. asiaticus*, with narrower nuchal collar and weaker spotting on wing-coverts; male of that species often has smaller white wing spots, and two outermost tail feathers are broadly tipped white. Slightly smaller than *C. indicus*, with wing-coverts less heavily spotted and fewer white tips to tail feathers in male. Slightly smaller, greyer and less variegated than *C. macrurus*, of which male has white tips to two outermost tail feathers. Immature similar to adult female but paler, greyer-brown. Two distinct racial groups differ significantly in size and colour: racial variation within smaller, greyer S populations (*affinis* group) includes overall coloration, colour of markings on upperparts, and amount of white on wings and tail; racial differences within larger, browner N populations (*monticolus* group) concern coloration only. Voice. Call is a loud, repetitive "chrip" or "chweep", given mainly in flight. Occasionally calls from perches. Other calls include low chuckles and soft screeches.

Habitat. Mainly grassland, grassy plains and open woodland and forest, often with scrub or rocky outcrops; also arable land, stony or sparsely vegetated hillsides and barren ridges, edges of swamps and mangroves, sandy or shingly beaches, bare sand or riverbanks, dry stony riverbeds with growth of scrub and grass, coastal scrubland, and urban habitats, including cities. Recorded from sea-level to 1500 m, possibly to 2000 m.

Food and Feeding. Diet includes moths, mantises, beetles, termites and flying ants. Forages in flight, often high above ground, hawking after prey over forests, cultivated areas, cities, towns, villages, airports and golf courses. Also feeds on insects attracted to artificial lights. Drinks in flight. Large feeding flocks often occur, especially during migration.

Breeding. Breeds Jun-Jul in N Pakistan, Apr-Aug in India and Himalayas, May to perhaps Mar in Philippines, Mar-Dec in Java, and Apr-Jan in Sumatra. Nest-site in open, at base of tree, hidden among scrub or tufts of grass, or beneath bush; no nest, eggs laid on ground, often among stones. Clutch 1-2 eggs, elliptical, salmon-pink or pale buffish, spotted and blotched reddish-brown and deep red; both sexes incubate, period not documented; adults threatened at nest-site perform injury-feigning distraction display; chick nidicolous, not described, fledging period not documented.

Movements. Poorly known. S populations that form *affinis* group appear to be largely sedentary, though a vagrant (possibly nominate race) recorded on Christmas I in May and Oct 1994 and possibly Nov 1996. Race *monticolus* sedentary and locally migratory, e.g. in NE Pakistan apparently a summer breeding visitor only, arriving Mar-Apr and departing Oct-Nov, probably moving through Punjab plains. Race *amoyensis* possibly sedentary. Race *stictomus* possibly sedentary and partially migratory, as some thought to move SW after breeding season and winter in Laos and SE Thailand.

Status and Conservation. Not globally threatened. Locally common to common throughout its range. Abundant passage migrant and common breeding bird in N Pakistan; probably not uncommon in SE China; resident in Taiwan; uncommon to locally common in N & C Thailand; locally common throughout much of Wallacea, Philippines and lowlands of Borneo; common in lowlands of Sumatra, Java and Bali. Tolerant of wide range of habitats and apparently highly adaptable; often occurs in urban environments, e.g. in W Indonesia frequents towns and cities in several regions of Sumatra and Java. Occurs in many protected areas throughout wide range, e.g. Chitwan National Park (Nepal), Panti Forest Reserve (Malaysia), Baluran National Park (Java) and Bali Barat National Park.

Bibliography. Ali (1996), Ali & Ripley (1983), Ali *et al.* (1996), Baker (1931), Chakravarty & Purna Chandra Tejasvi (1992), Cheng Tsolin (1987), Coates & Bishop (1997), Daniels *et al.* (1994), Deignan (1945), Delacour & Mayr (1946), Dickinson *et al.* (1991), Eames & Ericson (1996), Étchécopar & Hue (1978), Grimmett *et al.*

(1998), Harvey (1976, 1989), Hellebrekers & Hoogerwerf (1967), Higgins (1999), Holmes (1997), Holmes & Philipps (1996), Inskipp, C. & Inskipp (1991), Inskipp, T. *et al.* (1996), Jackson (1954), Johnstone *et al.* (1996), Jones (1923), Lekagul & Round (1991), Lim Kim Seng (1992), Lowther (1937), MacKinnon & Philipps (1993), Majumdar *et al.* (1992), van Marle & Voous (1988), Marshall (1978), Mayr (1944), McGregor (1905), Mukherjee (1995), Nash, S. V. & Nash (1985), Osmaston (1921a), Rajathurai (1996), Riley (1938), Ripley (1982), Roberts (1991), Round (1988), Saha & Dasgupta (1992), Severinghaus & Blackshaw (1976), Smythies (1981, 1986), Wardill (1995), Watling (1983), Wells (1999), Whistler (1921), Whistler & Kinnear (1935), White & Bruce (1986), Yang Lan *et al.* (1995), Zhao Zhengjie (1995).

73. Freckled Nightjar

Caprimulgus tristigma

French: Engoulevent pointillé **German:** Fleckennachtschwalbe **Spanish:** Chotacabras Pecosó
Other common names: West African Freckled Nightjar, Rock Nightjar

Taxonomy. *Caprimulgus tristigma* Rüppell, 1840, Gondar, Ethiopia.

Five subspecies recognized.

Subspecies and Distribution.

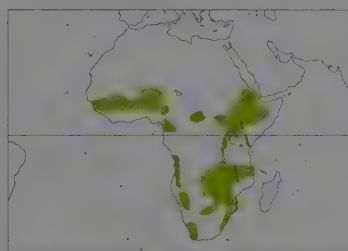
C. t. sharpei Alexander, 1901 - Guinea and N Sierra Leone E to W Nigeria, W Cameroon, N Equatorial Guinea and C Central African Republic.

C. t. pallidogriseus Parker & Benson, 1971 - Nigeria (perhaps on Jos Plateau).

C. t. tristigma Rüppell, 1840 - Ethiopia, S Sudan and NE Zaire S to Burundi and N Tanzania.

C. t. lentiginosus A. Smith, 1845 - W Angola, NW & WC Namibia and W South Africa.

C. t. granosus Clancey, 1965 - SE Zaire, Zambia and S Tanzania S to CN & E South Africa.



Descriptive notes. 26-28 cm; male 70-100 g, female 69-91 g. Sexually dimorphic. Upperparts and wing-coverts blackish-brown, profusely spotted and speckled white, pale buff and cinnamon, no nuchal collar; white throat patch; underparts dark brown barred whitish and cinnamon, becoming buff barred brown on belly. Male has small white spot on four outermost primaries and broad white tips to two outermost tail feathers; female has smaller white wing spots and lacks white in tail. Iris dark brown, bill blackish, legs and feet blackish. Immature similar to adult. Races vary slightly in size and tone of overall coloration. Voice.

Song of male is a variable "whow, whow, whow" or "ow-whow, ow-whow", although bursts of 4-5 notes may occasionally be given; also repetitive, ringing "wha" or "wa" sounds. Sings from rocks and occasionally other perches. Flight calls include "kheh, kheh, kheh" or a series of "wok" calls; if disturbed, utters "kluk, kluk, kluk" notes. Alarm call is a yelping gobble; adult gives soft, grumbling "gok, gok" calls during distraction displays; chick utters soft, mewing "wee-oo" sounds.

Habitat. Typically, rocky terrain with vegetation: outcrops, rocky or boulder-strewn hills, kopjes and inselbergs, ravines and wooded slopes on escarpments. Also bare hills within forest, on rocks alongside rivers and rapids, and more recently in built-up areas. Vacates burnt areas after fires. Outside breeding season, occasionally wanders away from rocky habitats. Recorded between 600 m and 2000 m.

Food and Feeding. Diet poorly studied. Feeds on moths, winged termites and beetles. Foraging methods not fully documented. Forages over rocks, rocky hillsides, open country and pastures; also hawks for insects around tree tops.

Breeding. Breeds Jan to perhaps May in Nigeria, May-Jun in Ethiopia, Kenya and NE Zaire, late Aug to Nov in Rwanda, Burundi, Tanzania, Zambia and Malawi, Aug-Dec in Zimbabwe, and Sept-Nov in South Africa and possibly S Mozambique. Possibly double-brooded, second clutch laid shortly after first brood fledges. Monogamous; territorial. Nest-site often near patches of lichen, in open or partly shaded, same site often used for several years; no nest, eggs laid usually on vegetation or leaf litter in depression or shallow hollow on rock, more recently also on flat rooftop (Durban, South Africa). Clutch usually 2 eggs, elliptical, whitish, streaked, speckled and blotched black, grey or light brown on underlying pale lilac, laid on successive days; incubation commences with first egg, is usually by female during day, period c. 17-19 days; adults threatened at nest-site give distraction display; chick semi-precocial, covered in mottled dark grey and off-white down, fed by regurgitation; young brooded for c. 12 days, fledge at c. 20 days.

Movements. Poorly known. Although appears to be mainly sedentary, some populations may undertake local movements in cold winters (e.g. at Matopos, Zimbabwe). Possibly migratory in Nigeria. No other information available.

Status and Conservation. Not globally threatened. Fairly common throughout much of range and locally abundant in some countries or regions. Uncommon and local in Ghana; locally fairly common in Togo; locally common in Nigeria in suitable habitat; extremely local but fairly common where it occurs in S Sudan; fairly common and locally abundant in Ethiopia. Local and possibly not particularly common in NE & SE Zaire; local in Uganda; locally uncommon to common in Kenya, though probably under-recorded; rather common locally in Zambia; fairly common in Malawi; widespread and locally very common in Zimbabwe; sparsely distributed and generally uncommon in N & E Botswana; locally common to very common in South Africa. Possibly more widespread than currently known. Occurs in several protected areas, e.g. Gashaka-Gumti Reserve (Nigeria), Tsavo West and Tsavo East National Parks and Marsabit Nature Reserve (Kenya), Akagera National Park (Rwanda) and Hwange National Park (Zimbabwe).

Bibliography. Bannerman (1953), Benson & Benson (1977), Benson & Pitman (1959), Benson *et al.* (1971), Britton (1980), Brouwer & Mullié (1992), Cave & Macdonald (1955), Cheke & Walsh (1996), Christy & Clarke (1994), Clancey (1957, 1972, 1996), Colebrook-Robjent (1979, 1984), Colston & Curry-Lindahl (1986), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Elgood (1972), Elgood *et al.* (1994), Field (1998), Fry *et al.* (1988), Gatter (1997), Ginn *et al.* (1989), Grimes (1987), Harrison *et al.* (1997), Hockey *et al.* (1989), Jackson (1971, 1973a, 1975, 1978, 1983, 1984a, 1986, 1987), Lewis & Pomeroy (1989), Lippens & Wille (1976), Louette (1981, 1990b), Mackworth-Præd & Grant (1957, 1962, 1970), Maclean (1993), Markus (1973), Masterson (1992), Nikolaus (1987, 1989), Parker & Benson (1971), Penny (1994), Pinto (1983), Rossouw & Cooper (1993), Short *et al.* (1990), Snow (1978), Steyn (1971, 1996a, 1996b), Urban & Brown (1971), Zimmermann, D.A. *et al.* (1996).

74. Bonaparte's Nightjar

Caprimulgus concretus

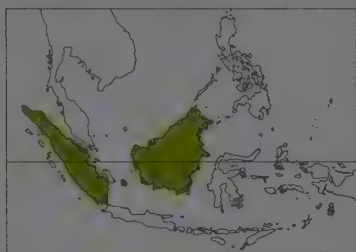
French: Engoulevent de Bonaparte

German: Sundanachtschwalbe

Spanish: Chotacabras de Bonaparte

Taxonomy. *Caprimulgus concretus* Bonaparte, 1850, Ashanti; error = Borneo. Monotypic.

Distribution. Sumatra, Belitung I and Borneo.



Descriptive notes. 21-22 cm. Sexually dimorphic. Upperparts brown spotted chestnut, no nuchal collar; wing-coverts brown, spotted chestnut and cinnamon; scapulars blackish-brown tipped chestnut, broadly edged pale buff on outer webs; white submoustachial stripe and large white throat patch; underparts brown barred chestnut, becoming buff barred brown on belly and flanks. Both sexes lack white on wings; male has white tips to two outermost tail feathers, female rarely having very narrow white tips. Iris dark brown, bill brownish, legs and feet brown. Paler and less heavily spotted than *C. pulchellus*, of which male has small white marks on four outermost primaries and white tips to two outermost tail feathers. Immature plumages unknown. Voice. Song of male is a low, mournful "wa-ouuuu", second note descending in pitch. Sings from perches, mainly at dusk and dawn and on moonlit nights.

Habitat. Mainly lowland forest: dipterocarp forest, heath forest and secondary growth, from sea-level to 500 m. One old record from cleared land in lowlands.

Food and Feeding. Diet poorly studied; probably feeds on insects. Foraging methods not fully documented. Forages by making short flycatching sallies from perches, often hunting out over rivers.

Breeding. No information.

Movements. None documented. Sedentary.

Status and Conservation. Not globally threatened. Currently considered Near-threatened. Although apparently widely distributed, species is possibly rare and under-recorded throughout its range. In Sumatra, no records since 1916 until several birds heard and seen in Way Kambas National Park in early Aug 1995. In Malaysian parts of Borneo: few recent records from Sarawak; only single record from Sabah, from 19th century.

Bibliography. Andrew (1992), Holmes (1996, 1997), Holmes & Burton (1987), MacKinnon & Philipps (1993), van Marle & Voous (1988), Marshall (1978), Parrott & Andrew (1996), Smythies (1981), Vowles & Vowles (1984), Yong (1997).

75. Salvadori's Nightjar

Caprimulgus pulchellus

French: Engoulevent de Salvadori

German: Salvadorinachtschwalbe

Spanish: Chotacabras de Salvadori

Taxonomy. *Caprimulgus pulchellus* Salvadori, 1879, Mount Singalan, Sumatra.

Races occasionally considered two separate species, and taxonomic status requires further study. Two subspecies currently recognized.

Subspecies and Distribution.

C. p. pulchellus Salvadori, 1879 - Sumatra.

C. p. bartelsi Finsch, 1902 - Java.



Descriptive notes. 19-21.5 cm. Sexually dimorphic, though not greatly so. Upperparts and wing-coverts dark brown, spotted and barred tawny, cinnamon and buff; crown and nape paler, greyer-brown, central feathers broadly streaked blackish; indistinct tawny-buff nuchal collar; tawny submoustachial stripe and large white patch on either side of lower throat; underparts tawny, buff and greyish-white, barred brown, becoming buff barred brown on lower belly, flanks and undertail-coverts. Male has small white spot or bar on second to fifth outermost primaries and white tips to two outermost tail feathers; female has tawny wing spots

and white or buff tips to two outermost tail feathers. Iris brown, bill blackish, tarsus brownish. Darker and more heavily spotted than *C. concretus*, which lacks white on wings in both sexes; race of that species has white tips to two outermost tail feathers. Immature plumages unknown. Race *bartelsi* rather similar but perhaps averages smaller; lacks nuchal collar, and has different scheme of coloration on upperparts. Voice. Song of male is possibly a short series of "tok" notes.

Habitat. Typically montane and submontane forest, often on cliffs and cliff faces; also occasionally in small marshy areas. Recorded between 800m and 2100 m.

Food and Feeding. Poorly studied. Probably feeds on insects; forages over forest clearings or near cliffs. When hunting, flies slowly with flapping wingbeats and frequent glides. Also makes short flycatching sallies from perches, or takes prey from cliff faces.

Breeding. Poorly known. Breeds late Mar to May in Java; season in Sumatra undocumented. Nest-site recorded under tea bush; no nest, eggs laid on leaf litter on ground. Clutch 1-2 eggs, elliptical, glossy white and unmarked.

Movements. None documented. Sedentary.

Status and Conservation. Not globally threatened. Data-deficient. Restricted-range species: present in Sumatra and Peninsular Malaysia EBA and Java and Bali Forests EBA. Although not currently listed as threatened, this poorly known species requires further study, especially in Sumatra. Only confirmed records from Sumatra are apparently the type specimen (a male), taken from Mt Singalang in Jul 1878, and another male taken from Gunung Dempo in Jul 1936, with sight records in Jun 1989 and Jul 1993. In Java, rare and little known, although a small population is known to exist in Gunung-Gede-Pangrango National Park.

Bibliography. Andrew (1985, 1992), Collar & Andrew (1988), Collar *et al.* (1994), Finsch (1902), Hellebrekers & Hoogerwerf (1967), Holmes (1996), Jany (1956), Kuroda (1936), MacKinnon (1988), MacKinnon & Philipps (1993), van Marle & Voous (1988), Marshall (1978), Nijman & Sözer (1996), Sargeant (1997), Stattersfield *et al.* (1998), Sujatnika *et al.* (1995).

76. Prigogine's Nightjar

Caprimulgus prigoginei

French: Engoulevent de Prigogine

German: Prigoginenachtschwalbe

Spanish: Chotacabras de Prigogine

Other common names: Itombwe Nightjar

Taxonomy. *Caprimulgus prigoginei* Louette, 1990, Malenge, Itombwe, Kivu Province, Zaire. Monotypic.

Distribution. E Zaire.



Descriptive notes. 19 cm. Known only from a single specimen, a female. Upperparts and wing-coverts brown, speckled and spotted dark brown, tawny and buff, no nuchal collar; breast brown spotted and barred tawny and buff; belly and flanks paler, barred brown; small tawny spot on second, third and fourth outermost primaries; narrow whitish tips to outermost tail feathers, narrower buffish or tawny tips to remainder. Iris not described, bill blackish, legs and feet reddish-brown. Voice. Unknown.

Habitat. Unknown, though probably a forest species. The single specimen is from 1280 m.

Food and Feeding. Probably feeds on insects.

Foraging methods unknown.

Breeding. Unknown.

Movements. Unknown.

Status and Conservation. VULNERABLE. Restricted-range species: present in Albertine Rift Mountains EBA. Currently known only from type specimen, a female, taken at Malenge, Itombwe, in Kivu Province, E Zaire in Aug 1955. Deforestation is a potential threat to this little-known species, although unidentified nightjars continue to be seen and heard in vicinity of type locality, and are also being reported from forests in other parts of Africa.

Bibliography. Collar *et al.* (1994), Curry-Lindahl (1960), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Dowsett-Lemaire & Dowsett (1998a), Louette (1990a), Stattersfield *et al.* (1998), Vuilleumier *et al.* (1992).

77. Collared Nightjar

Caprimulgus enarratus

French: Engoulevent à nuque rose

German: Halsband-Nachtschwalbe

Spanish: Chotacabras Acollarado

Taxonomy. *Caprimulgus enarratus* G. R. Gray, 1871, Madagascar.

Monotypic.

Distribution. Madagascar.



Descriptive notes. 24 cm; 1 female 54 g. Sexes similar. Upperparts greyish-brown boldly spotted blackish-brown, spots edged chestnut; broad rufous nuchal collar with thin, well-defined buff band above; wing-coverts greyish-brown boldly spotted blackish-brown, spots broadly edged chestnut or pale buff; scapulars greyish-brown, boldly spotted blackish-brown with chestnut edges; tawny-buff band around lower throat; underparts generally brownish, boldly spotted blackish-brown edged chestnut, becoming less spotted and more streaked on belly and flanks. Both sexes lack white markings on wings and have narrow white tips to one or two outermost tail feathers. Iris dark brown, bill blackish or pinkish-grey with black tip, legs and feet dark brown or pinkish-grey. Darker and plainer than *C. madagascariensis*, which usually has no or indistinct tawny-buff nuchal collar; male of that species has white spot on four outermost primaries and broad white tips to two outermost tail feathers. Juvenile of present species paler and buffier than adult, with dark collar around hindneck and row of large blackish spots across wing-coverts. Voice. Song of male unknown. Alarm calls of adult at nest are repetitive, liquid "kow" or "keow" notes; adult makes guttural hissing sounds during threat/defence displays; chick utters soft "chic" notes.

Habitat. Mainly lowland primary forest, including dense, humid, evergreen forest; also adjacent second-growth forest and occasionally dry, deciduous forest. Recently recorded in brush forest and mangroves in W Madagascar. Occurs from sea-level to 1880 m.

Food and Feeding. Poorly studied. Probably feeds mainly on insects. Forages by hawking for prey both above and below forest canopy. Also recorded flycatching from exposed perch c. 20 m above ground in clearing at edge of forest, with short foraging flights covering up to 10 m; one bout of flycatching lasted up to 15 minutes.

Breeding. Poorly known. Breeds late Sept to early Dec (mainly Oct-Nov). Nest-site usually at edge of forest track or clearing; no nest, eggs laid possibly on leaf litter on ground, or on epiphytic ferns (*Asplenium*) on tree trunk up to c. 1.7 m above ground, or to c. 1.5 m up in crown of free-standing ferns. Clutch 2 eggs, glossy white and often lightly washed pinkish-brown; incubation period not known; adults threatened at nest-site may give defence display or injury-feigning distraction display; chick covered with down but not further described, fledging period not known.

Movements. No movements documented. Probably sedentary.

Status and Conservation. Not globally threatened. Generally considered rather rare throughout much of range, though usually secretive and difficult to observe, so possibly under-recorded and locally uncommon to fairly common in some regions. Recorded from vicinity of Antananarivo, E Imerina, Fanovana, Sihanaka Forest, Nosibey-Foule Point, Cap Masoala, Andapa, Maroantsetra, Perinet-Analamazaotra, Ranomafana, Andohahela, Montagne d'Ambre, Ankarana, Tsaratanana, Anaborano, Sambirano and Manombo; may also occur in other areas such as Fort-Dauphin, Baly Bay and Morondava. Threats include hunting by local people and loss of habitat as a result of deforestation, although many sites where it occurs are now protected, e.g. Andohahela, Ankarafantsika and Tsaratanana Integral Nature Reserves, Marojejy Nature Reserve, and Perinet-Analamazaotra Special Reserve.

Bibliography. Benson *et al.* (1976-1977), Chittenden (1996), Dee (1986), Dhondt (1976), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Evans (1993), Goodman & Parrillo (1997), Goodman *et al.* (1997), Langrand (1995), Milon *et al.* (1973), Morris & Hawkins (1998), Rand (1936), Roxby (1998), Safford & Duckworth (1990).

78. Bates's Nightjar *Caprimulgus batesi*

French: Engoulevent de Bates **German:** Waldnachtschwalbe **Spanish:** Chotacabras de Bates
Other common names: (Bates's) Forest Nightjar

Taxonomy. *Caprimulgus batesi* Sharpe, 1906, River Dja, Cameroon.
Monotypic.

Distribution. W & S Cameroon, NE Gabon and W & NE Congo through SW Central African Republic and parts of Zaire to W Uganda.



Descriptive notes. 29-31 cm; (unsexed) 89-112 g. Sexually dimorphic. Upperparts and wing-coverts dark brown, broadly streaked, spotted and speckled blackish-brown, buff and tawny; buff or tawny nuchal collar; white throat patch; underparts blackish-brown, speckled buff on breast, becoming buff barred brown on belly. Male has small white spot on four outermost primaries and white tips to two outermost tail feathers; female is paler and lacks white markings on tail, those on wings being much duller. Iris, bill, legs and feet all dark brown. Immature similar to adult but paler and more buffish. **VOICE.** Song of male is a loud "whow, whow,

whow, whow", given from perches and occasionally ground. Flight call is a low "wuh wuh". **Habitat.** Mainly lowland primary rainforest, in clearings and along forest edges; also thick secondary forest, and plantations close to forest edges. Often near water and especially in flooded forest, where can be quite common in places.

Food and Feeding. Diet includes mantises, crickets, grasshoppers, beetles, moths and ants. Foraging methods poorly documented. Forages above and among forest canopy, along forest edges and over grassy plains.

Breeding. Poorly known. Breeds Dec-Jan in Gabon, Feb-Mar (possibly Nov-Jul) in Cameroon, and possibly all year in Zaire (Haut Zaire birds in breeding condition Mar-Oct, Lukokela egg Oct, Barumba chick Jul, and Evenaar juvenile Oct). Territorial. Nest-site on forest path or track, on sparsely vegetated ground, or along edge of thick forest, plantation or garden; no nest, egg laid on bare soil or leaf litter. Clutch 1 egg, elliptical, glossy white or pale pink, heavily blotched and mottled brown and lavender-grey; incubation period not known; chick covered in yellowish-buff down, fledging period not known.

Movements. None documented. Sedentary.

Status and Conservation. Not globally threatened. Considered potential candidate for listing as threatened species. Possibly locally common in rainforests throughout range. Locally common in N Congo; widely distributed but possibly rather rare in Cameroon, though present in protected areas such as Korup National Park; widely distributed in forested regions in Zaire. Territory size possibly up to c. 20 ha. Potential threat probably loss of habitat as a result of deforestation.

Bibliography. Bannerman (1953), Britton (1980), Brosset & Éard (1986), Carroll (1988), Carter & Colebrook-Robjent (1983), Christy & Clarke (1994), Dowsett & Dowsett-Lemaire (1991, 1993, 1997), Dowsett & Forbes-Watson (1993), Dowsett-Lemaire *et al.* (1993), Fry *et al.* (1988), Lippens & Wille (1976), Louette (1981, 1990b), Mackworth-Praed & Grant (1970), Rodewald *et al.* (1994), Sargeant (1993), Short *et al.* (1990), Snow (1978).

79. Long-tailed Nightjar *Caprimulgus climacurus*

French: Engoulevent à longue queue **German:** Schleppennachtschwalbe **Spanish:** Chotacabras Rabudo
Other common names: Slender-tailed Nightjar(!)

Taxonomy. *Caprimulgus climacurus* Vieillot, 1825, Senegal.

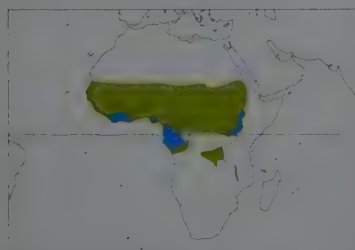
Forms superspecies with *C. clarus* and *C. fossii*, and all three have frequently been separated in genus *Scotornis*. Dark, dull-coloured birds from Sierra Leone to S Nigeria sometimes treated as separate race *leanini*, but possibly intermediate between nominate and race *sclateri*, or variant of latter. Three subspecies currently recognized.

Subspecies and Distribution.

C. c. climacurus Vieillot, 1825 - Mauritania E to W Ethiopia (except White Nile in S Sudan) and S to N & SE Zaire.

C. c. sclateri (Bates, 1927) - humid belt of W Africa (boundaries between races unclear).

C. c. nigricans (Salvadori, 1868) - White Nile in Sudan, from Kosti S to Shambe and L Nyubor; also along Bahr el Zeraf and Sobat R.



Descriptive notes. 28-43 cm; male 39-58 g, female 35-61 g. Sexually dimorphic. Variable in colour ranging from pale brown, brown and greyish-brown to sandy-buff. Upperparts and wing-coverts generally greyish-brown, finely streaked brown; male has white line across forewing, female having buff or buffish-white line; broad tawny or buff nuchal collar; white throat patch; underparts pale brown, speckled and barred pale buff, becoming buff thinly barred brown on belly and flanks. Male has broad white band across five outermost primaries and white trailing edge to inner wing, tail graduated, central pair longest, outer tail feathers edged and tipped white; female has buffish-white wing band and buff or buffish-white trailing edge to inner wing, and is shorter-tailed with outer feathers edged and tipped buff. Iris brown, bill brown, legs and feet brownish. Has notably longer tail than *C. clarus* and *C. fossii*, and is generally paler. Immature similar to adult female but paler. Race *nigricans* distinctive, generally blackish, male often longer-tailed; race *sclateri* more rufous, but variable in colour. **VOICE.** Song of male is a

long, evenly pitched churr, often ending with series of "chong" or "chiow" notes; sings from perches and ground. Calls include short series of "chong" or "chak" notes; makes guttural hissing sounds during threat/defence displays.

Habitat. Highly variable throughout range, in all habitats from arid semi-deserts to woods, forest and forest clearings; also commonly in all types of grassland and in cultivated areas. Also recently burnt areas and open patches in second growth and villages in Liberia. Outside breeding season, also stony hillsides and papyrus swamps.

Food and Feeding. Diet includes beetles, moths, mantises, bugs, ants, winged termites and grasshoppers. Foraging methods poorly studied. Forages in flight, hunting over open country, cultivated areas and among trees and bushes. Drinks in flight.

Breeding. Surprisingly poorly documented. Breeds Mar-Sept in N Senegal and possibly also Gambia, Mar-Aug in Mali and N Nigeria. Jan to perhaps Oct in S Nigeria. Feb-May in Sierra Leone, Jan-Dec in Ghana, possibly Feb-Aug in Togo, Mar-Jul in Uganda, Mar-Jun in N Zaire and Aug-Nov in SE Zaire. Probably monogamous. No nest, eggs laid on leaf litter or bare earth, often on or alongside path or track, in copse or cultivated field. Clutch usually 2 eggs, elliptical, creamy-white, buff or pinkish, heavily blotched grey or greyish-purple and stained amber; incubation and fledging periods not documented; downy chick not described.

Movements. Poorly known. Nominally race migratory and partially sedentary, some populations moving S after breeding season. Race *sclateri* possibly sedentary and partially migratory. Race *nigricans* probably sedentary. Outside breeding season, range also includes S Ivory Coast, SW Nigeria, S Cameroon, Equatorial Guinea, Gabon, SE Congo (lower Congo river valley), NE Angola (one record Luaco), SE Sudan, SW Ethiopia, W Kenya (sporadic in Turkana and Pokot region) and E Uganda.

Status and Conservation. Not globally threatened. Common and locally abundant throughout much of range, perhaps less so in forest clearings in S. Widespread and often rather common in Senegal; locally common in Gambia; common in Ghana and Togo; fairly common breeding visitor to Niger; Locally abundant on S shores of L Chad; widespread and common in Nigeria, numbers in S swollen by N migrants Nov-Feb; common and widely distributed throughout much of Sudan. Common in N Congo; widely distributed in Zaire; rare to scarce locally in Kenya. Occurs in several protected areas, e.g. Djoudj and Niokola Koba National Parks (Senegal), W National Park (Niger) and Waza National Park (Cameroon).

Bibliography. Bannerman (1953), Barlow *et al.* (1997), Bates (1927), Britton (1980), Brouwer (1992), Brown & Britton (1980), Cave & Macdonald (1955), Chapin (1939), Cheke & Walsh (1996), Colston & Curry-Lindahl (1986), Demy & Fishpool (1991), Dowsett & Dowsett-Lemaire (1993, 1997), Dowsett & Forbes-Watson (1993), Elgood, Fry & Dowsett (1973), Elgood, Heigham *et al.* (1994), Field (1998), Fry (1988a), Fry *et al.* (1988), Gatter (1997), Giraudoux *et al.* (1988), Gore (1990), Grimes (1987), Herremans & Stevens (1983), Jensen & Kirkeby (1980), Lewis & Pomeroy (1989), Lippens & Wille (1976), Louette (1981, 1990b), Mackworth-Praed & Grant (1957, 1970), Morel & Morel (1990), Newby (1980), Nikolaus (1987, 1989), Pinto (1983), Pitman (1930a, 1930b), Rand (1951b), Short *et al.* (1990), Smith (1957), Snow (1978), Tye (1984), Urban & Brown (1971), Zimmerman, D.A. *et al.* (1996).

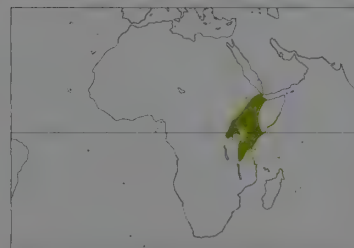
80. Slender-tailed Nightjar *Caprimulgus clarus*

French: Engoulevent de Reichenow **Spanish:** Chotacabras Colifino
German: Kurzschleppen-Nachtschwalbe
Other common names: Reichenow's Nightjar

Taxonomy. *Caprimulgus clarus* Reichenow, 1892, Bukoba Tanzania.

Formerly considered conspecific with *C. fossii*, and these two form superspecies with *C. climacurus*; all three have frequently been separated in genus *Scotornis*. N populations formerly awarded separate race, *apatilis*. Monotypic.

Distribution. Djibouti, Ethiopia and SE Sudan S to Tanzania.



Descriptive notes. 28 cm; male 36-49 g, female 34-53 g. Sexually dimorphic. Slight colour variation with dark brown, blackish or buffish individuals noted. Upperparts and wing-coverts generally greyish-brown streaked dark brown; male has white line across forewing, female has buffish line; broad tawny or buff nuchal collar; white throat patch; underparts light brown, speckled and barred pale buff, becoming buff thinly barred brown on belly and flanks. Male has broad white band across six outermost primaries and white trailing edge to inner wing, tail graduated and wedge-shaped, central feathers longest, outer

feathers edged and tipped white; female has narrower white wing bands, buff or buffish-white trailing edge to inner wing, and tail less graduated with outer feathers edged and tipped buff. Iris brown, bill brown with black tip, legs and feet brownish. Has much shorter tail than *C. climacurus*, which is more variable in colour. Paler and greyer than *C. fossii*, with weaker streaking on crown, and longer tail much more graduated. Immature similar to adult female but paler. **VOICE.** Song of male is a long series of rapid "wa, wa, wa, wa, wa" notes, perhaps forming a slow churr, occasionally interspersed with high-pitched "wee" calls and ending with "chor-chor" or bubbling notes. Sings from ground or occasionally from perches. Flight call is a treble-noted "whit, whit, whit".

Habitat. Mainly thorny bush country, acacia scrub, sparsely wooded grassland, thinly vegetated scrubland, and open woodland, from sea-level to 2000 m.

Food and Feeding. Diet includes moths, flies, beetles, ants, bugs and Orthoptera. Foraging methods poorly studied. Forages by hawking for prey low over open ground, grasslands and rocky slopes. Also feeds on insects attracted to artificial lights.

Breeding. Poorly documented. Generally breeds Feb-May throughout range, N populations possibly beginning earlier, e.g. Feb-Mar in Ethiopia, Mar-Apr (also Jun-Aug) in Uganda, and Apr-May (also Nov) in Kenya. Possibly monogamous. No nest, eggs laid on bare soil, usually near or below small bush, occasionally near rock or stone. Clutch usually 2 eggs, elliptical, creamy or pinkish, blotched brown and faintly marked greyish-lilac; incubation period not known; adults threatened at nest-site may perform injury-feigning display; downy chick not described, fledging period not known.

Movements. Poorly known. Possibly sedentary throughout much of range, although in Somalia may be locally migratory according to rains.

Status and Conservation. Not globally threatened. Common to locally abundant throughout range. Common to abundant in Ethiopia, especially in S; locally abundant in S Somalia; widely distributed and locally common to abundant in SE Sudan, Uganda, Kenya and NE Tanzania. Occurs in several

ers edged and tipped white; female has buffish-white wing band and buff or buffish-white trailing edge to inner wing, and is shorter-tailed with outer feathers edged and tipped buff. Iris brown, bill brown, legs and feet brownish. Has notably longer tail than *C. clarus* and *C. fossii*, and is generally paler. Immature similar to adult female but paler. Race *nigricans* distinctive, generally blackish, male often longer-tailed; race *sclateri* more rufous, but variable in colour. **VOICE.** Song of male is a

protected areas, e.g. Awash National Park (Ethiopia), Samburu and Masai Mara Reserves (Kenya) and Tarangire National Park (Tanzania).

Bibliography. Archer & Godman (1937-1961), Ash & Miskell (1983b, 1998), Britton (1980), Brown & Britton (1980), Cave & Macdonald (1955), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Duckworth *et al.* (1992), Friedmann (1930), Fry *et al.* (1988), Lewis & Pomeroy (1989), Louette (1990b), Mackworth-Praed & Grant (1957), Nikolaus (1987, 1989), Peters & Loveridge (1936), Schels & Lavoyer (1987), Short *et al.* (1990), Snow (1978), van Someren (1956), Urban & Brown (1971), Wilson & Wilson (1994), Zimmerman, D.A. *et al.* (1996).

81. Mozambique Nightjar

Caprimulgus fossii

French: Engoulevent du Mozambique

German: Weltschnachtschwalbe

Spanish: Chotacabras de Fosse

Other common names: Gabon/Gaboon/Square-tailed Nightjar

Taxonomy. *Caprimulgus Fossii* Hartlaub, 1857, Gabon.

Formerly considered conspecific with *C. clarus*, and these two form superspecies with *C. climacurus*; all three have frequently been separated in genus *Scotornis*. In past, birds of coastal E Africa sometimes placed in race *mossambicus*. Three subspecies currently recognized.

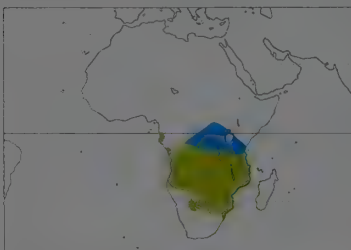
Subspecies and Distribution.

C. f. fossii Hartlaub, 1857 - N & SW Gabon, and possibly SW Congo.

C. f. welwitschii Bocage, 1867 - S Zaire, S Burundi and S Tanzania S to N Namibia, N & E Botswana and NE South Africa.

C. f. griseoplurus Clancey, 1965 - Kalahari Desert and extreme N South Africa.

Non-breeding visitor N to N Zaire, Uganda and S Kenya.



Descriptive notes. 23-24 cm; male 54-68 g, female 47-77 g. Sexually dimorphic. Upperparts generally dark greyish-brown, heavily speckled greyish-white; broad buff or tawny-buff nuchal collar; wing-coverts dark greyish-brown, speckled and spotted greyish-white and pale buff; male has white, occasionally buffish, band across forewing, female has buff band; scapulars blackish-brown, broadly edged buff on outer webs; prominent buffish-white submoustachial stripe and white throat patch; underparts dark greyish-brown, speckled and spotted buffish-white or buff, becoming buff barred brown on belly and flanks. Male has

broad white band across five outermost primaries, white trailing edge to inner wing, and outermost tail feathers broadly edged and tipped white; female has narrower, whitish wing bands, buff trailing edge to inner wing, and outermost tail feathers broadly edged and tipped buff. Iris brown, bill blackish, legs and feet fleshy-brown or blackish. Darker and browner than *C. clarus*, with heavier streaking on crown, and a less graduated tail. Has much shorter tail than *C. climacurus*, which is more variable in colour. Immature similar to adult female but paler and plainer. Race *welwitschii* is

generally larger with heavier spotting on wing-coverts, and variable in colour, ranging from buffish-brown to blackish-brown. Race *griseoplurus* is larger, greyer and paler. **VOICE.** Song of male is a distinctive churr that rises in pitch and then levels off, occasionally ending with a single "wow" note. Sings from ground and occasionally perches. Calls include series of short "a-whoow" notes in flight, "whit, joe" while perched, and a rapid "shwip-ip-ip-ip" when alarmed; male makes guttural hissing or growling sounds during territorial encounters with other males; adults and chicks make guttural hissing sounds during threat/defence displays.

Habitat. Mainly open woodland or scrub, wooded grassland, and sandy country near water: mopane woodland and scrubland, open miombo woodland, riverine forest, wooded suburban gardens and thorny bush country. Also woodland edges, wooded hillsides, edges of cultivated land, urban gardens, plantations, teak forest, stony hillsides with scattered vegetation, burnt vleis, treeless dambos, savanna, swamps, trampled reedbeds, and lower slopes of kopjes. Recorded from sea-level to 1850 m.

Food and Feeding. Diet includes moths, beetles, grasshoppers, winged termites, ants and bugs. Forages by hawking for prey low over ground or water. Also makes short flycatching sallies from ground or perches, and may feed on insects attracted to or disturbed by fires.

Breeding. Breeds Jun on Pemba I, Oct on Zanzibar, Sept-Dec in S Burundi, S Tanzania and Mozambique, Sept-Nov in Malawi, Zambia and Zimbabwe, Oct-Jan in S Zaire, Aug-Oct in Angola, and Sept-Dec in Botswana and South Africa. Possibly single-brooded. Monogamous; probably territorial. Nest-site often among bushes or scattered clumps of grass, on burnt ground or near water, also on slope of kopje; no nest, eggs laid on leaf litter, bare soil, sand or gravel. Clutch 1-2 eggs, elliptical, matt or glossy, creamy-pink, blotched and smeared brown, finely speckled grey and lilac-grey, markings denser around blunt end; lays replacement clutch if first is lost; incubation mainly by female, period generally 14-17 days; chick semi-precocial, covered in dark brown and buffish down; adults threatened at nest-site may perform distraction display; fledging period not documented.

Movements. N nominate race probably sedentary. Race *welwitschii* possibly sedentary in parts of range, partially migratory in others, as only a breeding visitor to central plateau of Zimbabwe and parts of NE South Africa. As a non-breeding (winter) visitor, occurs in N Zaire, N Burundi, Rwanda, S & W Uganda, S Kenya and N Tanzania. Possible vagrant to S Botswana and C South Africa. Race *griseoplurus* also sedentary and partially migratory; occurs as a non-breeding (winter) visitor to Angola and Zambia, and as a possible vagrant to N Zimbabwe. Vagrants of unidentified race recorded in N Ivory Coast and S Ghana.

Status and Conservation. Not globally threatened. Very common to locally abundant throughout much of range. Locally common (perhaps seasonally) in S Kenya; widespread and common in S Zaire, C & S Tanzania, Zanzibar and Pemba. Widespread and common in Angola; locally abundant in Zambia; very common in Malawi, though less so above 650 m; generally very common in Mozambique; common throughout much of Zimbabwe, though less so Jun-Sept; common in N Namibia; common but sparsely distributed in Botswana, perhaps mainly in N & E; common in lowlands of NE South Africa, less common at higher altitudes. Occurs in a number of protected areas, e.g. Ruvuvu National Park (Burundi), Liwonde National Park (Malawi) and Kafue National Park (Zambia). Status of *griseoplurus* uncertain; recent surveys could not locate these populations in Kalahari.

Bibliography. Bannerman (1953), Benson & Benson (1977), Benson *et al.* (1971), Britton (1980), Brown & Britton (1980), Clancey (1965, 1996), Colebrook-Robjent (1979, 1984), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Fry *et al.* (1988), Ginn *et al.* (1989), Hanmer (1996), Harrison *et al.* (1997), Jackson (1971, 1975, 1978, 1983, 1984a, 1986, 1987), Lewis & Pomeroy (1989), Lippens & Wille (1976), Louette (1990b), Mackworth-Praed & Grant (1957, 1962, 1970), Maclean (1993), Pakenham (1979), Penry (1994), Pinto (1983), Short *et al.* (1990), Snow (1978), Steyn (1996a, 1996b), Tree (1992), Zimmerman, D.A. *et al.* (1996).



82

83

84

85

PLATE 35

inches 4
cm 10

ssp torquata

ssp furcifera

Genus *MACRODIPTERYX* Swainson, 1837

82. Standard-winged Nightjar

Macrodipteryx longipennis

French: Engoulevent à balanciers

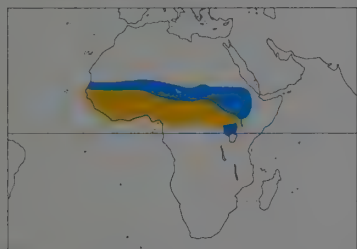
Spanish: Chotacabras Portaestandard

German: Fahnennachtschwalbe

Taxonomy. *Caprimulgus longipennis* Shaw, 1796. Sierra Leone.

Genus formerly considered monotypic, with *M. vexillarius* separated from present species in genus *Semeiophorus*; however, despite the evident differences in morphology, the two species show notable similarities in vocalizations, breeding strategy, and some roosting and feeding habits, as well as a number of morphological affinities, and so are probably best considered congeneric. Monotypic.

Distribution. Gambia and W Liberia through C Cameroon and N Zaire to SW Sudan, N Uganda and possibly NW Kenya; present in dry season in coastal strip from E Liberia to W Cameroon, and in SE Uganda (Dec-Mar), but breeding not confirmed in these areas. Winters in Sahel zone N of breeding range.



Descriptive notes. 21-22 cm (excluding male's "standards", which reach 45-53.5 cm in length); male 32-65 g, female 32-65 g. Sexually dimorphic, breeding males unmistakable, with strikingly spectacular "standards" on wings. Variable in coloration, male often blacker with whiter speckling, female often buffier or sandier. Upperparts brown speckled greyish-white, crown also speckled buff or tawny, and boldly spotted blackish-brown; broad tawny or tawny-buff nuchal collar; wing-coverts brown, speckled greyish-white and pale tawny and heavily spotted buff; scapulars blackish-brown, broadly edged buff;

supercilium buff, but rather short; throat patch buff barred brown; underparts brown, speckled greyish-white, speckled and spotted buff, becoming buff barred brown on belly and flanks. Both sexes lack white markings on wings and tail. Breeding male has extremely elongated second innermost primaries, which are webbed at tips only, forming "standards" or flags. Iris dark brown, bill blackish, legs and feet dark brown. Smaller than *M. vexillarius*; female slightly smaller and paler with paler nuchal collar and shorter supercilium, lacks white throat patch and has less strongly barred underparts. Immature similar to adult female. **VOICE.** Song of male is a rapid series of soft, high-pitched "ts" notes; also slower, harsher "s-ch" notes. Sings from ground or perches or in display flights. Calls include soft "ch" or "tsui" and low "cuk" notes.

Habitat. Typically occurs in lightly wooded savanna, or savanna with bush or thorn scrub. Also farmland in thickly wooded savanna, open grassy terrain, stony hillsides with scattered trees and vegetation, coastal plains and sandy wastelands; less commonly, pastures, thorn thickets, clearings (often near villages), grassy inselbergs within forest, lawns and paved areas. Recorded from sea-level to 1400 m.

Food and Feeding. Diet includes beetles, moths, grasshoppers, cicadas, earwigs, bugs, leafhoppers, flies, winged ants, winged termites and mosquitoes. Foraging methods poorly described. Forages by hawking for prey over open country and along roadsides and tracks. Also feeds at insect swarms and on insects disturbed by fires.

Breeding. Breeds Mar-Jul in Senegal and Gambia, Nov-Jul in Mali, Feb-May in Liberia and possibly also Togo, Jan-May in Ghana, Jan-Jun in Nigeria. Sept and Feb-Apr in N Uganda, and late Jan to early Apr in N Zaire; periods may be longer than stated, and possibly influenced by rains; S populations breed earlier than N. Polygamous; solitary or semi-colonial; possibly not territorial. Nest-site near vegetation, in grass tussock or clump of small trees, or in open; no nest, eggs laid directly on ground, typically on bare, sandy soil. Males and females gather at display arenas in open spaces. Clutch 1-2 eggs, elliptical, slightly glossy, pinkish-buff, salmon-pink or reddish-chestnut, smeared and spotted brown and grey, laid on successive days; incubation begins with first egg and is mainly by female; chick semi-precocial, covered in buffish down, mottled black on upperparts; female threatened at nest-site may perform injury-feigning distraction display; incubation and fledging periods not documented.

Movements. An intra-African migrant, movements protracted and possibly influenced by rains, not fully understood. Leaves breeding grounds in southern savannas of W & C Africa from mid-Apr to about Aug and moves N to spend wet season in savannas of Sahel and Sudan. E populations move E or NE from Apr. Occurs possibly Aug-Dec in S Mauritania, N Senegal, C Mali, S Niger, N Nigeria and C Chad (N to Ennedi Mts). Also recorded in C & SE Sudan (perhaps mid-Apr to Sept) and W Ethiopia (up to Jan), Uganda and W Kenya. Return movements poorly known. Probable vagrants recorded in W Kenya and N Somalia.

Status and Conservation. Not globally threatened. Widespread and frequent to abundant throughout much of breeding range. Fairly common to abundant from Senegal, Gambia and Sierra Leone E to S Sudan, NW Uganda and NE Zaire; widely distributed in Senegal; locally common in Gambia; not uncommon in Ghana; seasonally common in savanna zone in Togo. Outside breeding season, locally numerous in S Mauritania (late Sept to Oct) and S Niger, uncommon to locally frequent in W & S Ethiopia; rare seasonal visitor to W Kenya; seasonally common intra-African migrant in Nigeria. No data available from other regions. Occurs in a number of protected areas throughout range, e.g. Niokola Koba National Park (Senegal), Gola Forest Reserves (Sierra Leone), W National Park (Niger), Bamingui-Bangoran and Manovo-Gounda-Saint-Floris National Parks (Central African Republic), Kabalega Falls National Park (Uganda) and Awash National Park (Ethiopia).

Bibliography. Archer & Godman (1937-1961), Bannerman (1933, 1953), Barlow *et al.* (1997), Britton (1980), Brouwer (1992), Cave & Macdonald (1955), Chapin (1939), Cheesman & Sclater (1935), Cheke & Walsh (1996), Colston & Curry-Lindahl (1986), Dorst *et al.* (1975), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Elgood, Fry & Dowsett (1973), Elgood, Heigham *et al.* (1994), Field (1998), Fry (1969), Fry *et al.* (1988), Gatter (1997), Giraudoux *et al.* (1988), Gore (1990), Grimes (1987), Harwin (1994), Jackson (1984c, 1985b), Lewis & Pomeroy (1989), Lippens & Wille (1976), Louette (1981, 1990b), Mackworth-Præd & Grant

(1957, 1970), Morel & Morel (1990), Nikolaus (1987, 1989), Rand (1951b), Short *et al.* (1990), Snow, D.W. (1978, 1979), Stresemann & Stresemann (1966), Urban & Brown (1971), Woodell & Newton (1975), Zimmerman, D.A. *et al.* (1996).

83. Pennant-winged Nightjar

Macrodipteryx vexillarius

French: Engoulevent porte-étendard

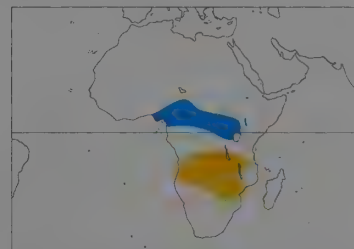
German: Flaggennachtschwalbe

Spanish: Chotacabras Cuelgacintas

Taxonomy. *Semeiophorus* (*Macrodipteryx*?) *vexillarius* Gould, 1838, Sierra Leone.

Formerly isolated in monotypic genus *Semeiophorus*; however, despite the evident differences in morphology, the two species show notable similarities in vocalizations, breeding strategy, and some roosting and feeding habits, as well as a number of morphological affinities, and so are probably best considered congeneric. Specific name has at times been incorrectly given as *vexillaria*, but *vexillarius* originally described as masculine noun in apposition to masculine genus name. Validity of type locality is questionable, although vagrants have been recorded in several parts of W Africa. Monotypic.

Distribution. C, NE & E Angola, S Zaire and SW Tanzania S to NE Botswana, NE Namibia (Caprivi Strip) and extreme NE South Africa. Winters from SE Nigeria to Uganda.



Descriptive notes. 24-28 cm (excluding male's "pennants", which reach 48-78 cm in length); male 59-79 g, female 65-88 g. Sexually dimorphic, breeding males unmistakable, with strikingly spectacular "pennants" on wings. Upperparts brown, speckled and barred greyish-brown, greyish-white and buff, crown also boldly spotted blackish-brown; broad tawny nuchal collar; wing-coverts brown, speckled buff and greyish-white, speckled and spotted tawny; scapulars generally blackish-brown on inner webs, buff on outer webs; supercilium buff and rather long; throat patch white; underparts brown, tinged and spotted

tawny or tawny-buff, becoming white (male) or buff (female), barred brown, on belly and flanks. Male has blackish wings, narrow white tips to four outermost primaries, white trailing edge to inner wing, and broad white band across eight outer primaries; breeding male has second innermost primaries extremely elongated and generally whitish, forming "pennants"; female has brown wings, broadly barred tawny, and both sexes lack white markings on tail. Iris dark brown, bill blackish-brown, legs and feet pinkish-brown or greyish-brown. Larger than *M. longipennis* is smaller, with female slightly darker with darker nuchal collar, and longer supercilium, buff throat patch and less strongly barred underparts. Immature similar to adult female but paler. **VOICE.** Song of male is a series of rapid, high-pitched "tset" notes given in display flights or from perches. Flight calls are querulous "wheeo" or "chup" notes. Female may utter soft "schurr" calls prior to copulation.

Habitat. Mainly mature miombo or mopane woodland, also other woodland (including burnt or cleared), wooded grassland, open grassland within woodland, bush country, wooded suburban areas, cultivation, disused agricultural areas and gardens, river valleys, burnt open dambos and burnt vleis; also stony hillsides, sandy terrain and teak forest. Tends to avoid acacia bush and thornveld. On passage also in forest clearings and openings, and on wintering grounds also in eucalyptus plantations. Recorded from sea-level to 2800 m.

Food and Feeding. Diet includes moths, beetles, winged termites and ants, crickets, grasshoppers, mantids, cockroaches, earwigs, shield bugs, leafhoppers and cicadas. Forages by hawking for prey in flight, often hunting high above ground. Also makes flycatching sallies from ground. Occasionally forages by day. During non-breeding season, flocks of up to 30 may feed together. Drinks in flight.

Breeding. Breeds Aug-Oct in Angola, late Aug to Nov in Zambia, Aug-Mar in S Tanzania, Oct-Dec in Malawi, Mozambique and Zimbabwe, and Sept-Nov (possibly Dec) in South Africa. Single-brooded. Polygamous; possibly territorial at courtship display arena, but not at nesting site; in some regions semi-colonial, with nests 6.3-19.5 m apart. Nest-site in open or shaded by trees, quite often on burnt ground; no nest, eggs laid on bare ground or leaf litter. Males perform courtship display flights. Clutch 1-2 eggs, elliptical, rounded or almost biconical, glossy, pale to deep salmon-pink, marbled, blotched and spotted dark pink, reddish-brown, violet and grey, laid 1-2 days apart; incubation usually by female, begins with first egg, period 15-18 days; downy chick not described; fledging period not documented.

Movements. An intra-African, transequatorial migrant, although movements rather protracted and not fully understood. After breeding, large flocks may gather prior to migration; often migrates in single-sex flocks, though also in pairs. Leaves breeding grounds Feb-Apr and moves N through S Cameroon, Gabon, Congo, C Zaire, Burundi, Tanzania and SW Kenya. Wintering range (Feb-Oct) apparently SE Nigeria, N & C Cameroon, SW Chad (also Nov record), Central African Republic (possibly except NE), N & NE Zaire, S Sudan and Uganda. Return movements S occur Jul-Oct. Movements occasionally irruptive at times. During N movements and non-breeding season, possible vagrants recorded in Gambia, Guinea Bissau, S Ghana, Togo, SW and NE Nigeria, SW Niger, SE Chad, W Sudan (possibly regular in Darfur), E Sudan and S Somalia. During S movements and breeding season, possible vagrants recorded in N Namibia, W Botswana and South Africa.

Status and Conservation. Not globally threatened. Common to locally abundant throughout much of breeding range, from C Angola E through S Zaire to SW Tanzania, S to NE South Africa. Extremely common to locally abundant in Zambia; very common in Malawi; locally common throughout Zimbabwe; sparsely distributed in Botswana; listed as indeterminate in South African Red Data Book. An uncommon transequatorial migrant in Nigeria; uncommon in Gabon; a common passage migrant across N Congo and much of Zaire; uncommon in Burundi; locally and seasonally scarce to casual in W Kenya; probably not common in Tanzania. Occurs in several protected areas, e.g. Bamingui-Bangoran and Manovo-Gounda-Saint-Floris National Parks (Central African Republic), Kabalega Falls National Park (Uganda), Akagera National Park (Rwanda), Ruvuvu National Park (Burundi) and Kafue National Park (Zambia).

Bibliography. Bannerman (1933, 1953), Benson & Benson (1977), Benson *et al.* (1971), Bowen (1977b), Britton (1969, 1980), Brooke (1984), Cave & Macdonald (1955), Chapin (1916, 1939), Chenaux-Repond (1971), Clancey

(1996). Colebrook-Robjent (1979, 1984), Dowsett & Dowsett-Lemaire (1993, 1997), Dowsett & Forbes-Watson (1993), Elgood *et al.* (1994), Fry *et al.* (1988), Ginn *et al.* (1989), Hanmer (1996), Harrison *et al.* (1997), Harwin (1984, 1994), Jackson (1971, 1975, 1978, 1984a, 1985b, 1986), Lewis & Pomeroy (1989), Lippens & Wille (1976), Louette (1990b), Mackworth-Praed & Grant (1957, 1962, 1970), Maclean (1993), Nikolaus (1987), Penry (1994), Pinto (1983), Priest (1934), Rockingham-Gill (1982), Shaw (1991, 1993), Short *et al.* (1990), Snow, D.W. (1978, 1979), Steyn (1996a, 1996b), Stresemann & Stresemann (1966), Tree (1967, 1975), Zimmerman, D.A. *et al.* (1996).

Genus *HYDROPSALIS* Wagler, 1832

84. Ladder-tailed Nightjar

Hydropsalis climacocerca

French: Engoulevent trifle

Spanish: Chotacabras de Escalera

German: Staffelschwanz-Nachtschwalbe

Taxonomy. *Caprimulgus climacocercus* Tschudi, 1844, Peru. Validity of races *intercedens*, *pallidior* and *canescens* questionable, as all three occur along a 120-km stretch of the lower Amazon between Obidos and Santarém, and all remain virtually unknown. Five subspecies currently recognized.

Subspecies and Distribution.

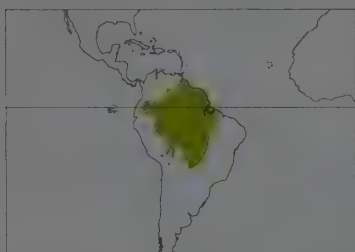
H. c. schomburgki P. L. Slater, 1866 - E Venezuela and the Guianas.

H. c. climacocerca (Tschudi, 1844) - SE & E Colombia to S Venezuela, and S to N & E Bolivia.

H. c. intercedens Todd, 1937 - NC Brazil: known only from type locality at Obidos in W Pará.

H. c. pallidior Todd, 1937 - NC Brazil: known only from type locality at Santarém in W Pará.

H. c. canescens Griscom & Greenway, 1937 - NC Brazil: known only from lower Tapajós in W Pará.



Descriptive notes. 24-26 cm; male 42-46 g, female 45-52 g. Sexually dimorphic. Upperparts greyish-brown or brownish, streaked blackish-brown; buffish nuchal collar; wing-coverts brown or greyish-brown, boldly spotted buffish; scapulars blackish-brown, broadly edged buff on outer webs; white submoustachial stripe and white (male) or buffish (female) throat patch; underparts greyish-brown or brown, barred and spotted buff, becoming buff barred brown on belly and flanks. Male has broad white band across four outermost primaries and much white in tail; female has narrower white wing bands and

rarely shows white in tail. Iris dark brown, bill blackish, legs and feet brownish. Slightly smaller and paler than *H. torquata*, with duller nuchal collar and prominent white wing bands; male has much shorter tail. Immature similar to adult female. Racial variation often slight, involving size and overall coloration. Voice. Song, or perhaps call, is a repetitive, high-pitched "chip". Calls include soft, musical "chewit" or "cheeit" notes.

Habitat. Typically, rainforest, open woodland, secondary growth, riverine forest and grassland, on riverbanks, sandbars, and stones and rocks in rivers; also in areas with thickets. Lowland species, recorded from sea-level to 500 m.

Food and Feeding. Diet poorly studied, but probably feeds on insects. Foraging methods poorly documented. Forages by making short sallies from low perches or sandbars, hawking after prey along river edges.

Breeding. Poorly known. Breeds possibly late Jul to Aug (probably longer) in Colombia and Dec-Feb in Brazil (NW Amazonas); no data from other regions. Nest-site on mudflats, sand, or among driftwood, usually shaded by vegetation; no nest, eggs laid on sand or bare soil. Clutch 2 eggs, elliptical, olive-drab, speckled, spotted and scrawled grey and brown; incubation and fledging periods not known; downy chick not described.

Movements. None documented. Sedentary.

Status and Conservation. Not globally threatened. In Colombia, common along large rivers where there are sandbars and river islands. In Surinam, common along rivers where there are plenty of rocks and stones. No data available from other countries. Occurs in Amacayacu National Park (Colombia) and Tambopata Reserve (Peru).

Bibliography. Allen (1995), Blake (1950b), Butler (1979), Chebez (1994), Davis *et al.* (1994), Donahue (1994), Friedmann (1948), Griscom & Greenway (1937), Haverschmidt & Mees (1994), Hilty & Brown (1986), Hoy

(1987), Meyer de Schauensee & Phelps (1978), Parker *et al.* (1982), Remsen & Traylor (1989), Schubart *et al.* (1965), Sick (1993, 1997), Snyder (1966), Stotz *et al.* (1996), Todd (1937a), Tostain *et al.* (1992).

85. Scissor-tailed Nightjar

Hydropsalis torquata

French: Engoulevent à queue en ciseaux

Spanish: Chotacabras Tijereta

German: Scherenschwanz-Nachtschwalbe

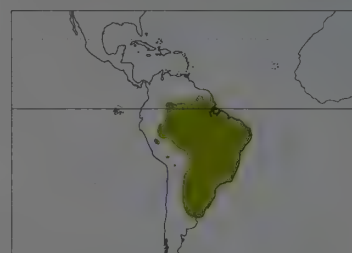
Taxonomy. *Caprimulgus torquatus* J. F. Gmelin, 1789, Brazil.

Species name has normally been given as *brasiliensis*, but this name is based on a drawing and a written description, and is not clearly identifiable as present species, indeed some points would appear to preclude this: *torquata*, proposed by same author on the following page of the same publication, was consistently used in Brazilian literature until 1966, and should be reinstated. Two subspecies recognized.

Subspecies and Distribution.

H. t. torquata (J. F. Gmelin, 1789) - S Surinam, EC Peru and Brazil.

H. t. furcifera (Vieillot, 1817) - N & E Bolivia, S Brazil, Paraguay, N & C Argentina and Uruguay.



Descriptive notes. 25-30 cm (excluding outer tail feathers of male, which reach 27-36 cm in length); male 47-52 g, female 48-75 g. Sexually dimorphic. Upperparts brown streaked blackish-brown; broad tawny or buff nuchal collar; wing-coverts brown, heavily spotted buff and greyish-white, with distinct buffish line along scapulars; thin whitish submoustachial stripe; throat pale but no obvious white patch; underparts brown, barred and spotted buff, becoming pale buff or buffish-white barred brown on belly and flanks. Both sexes lack white markings on wings. Male has much elongated whitish outermost tail feathers edged

brown; female has shorter tail that lacks white. Iris dark brown, bill dark brown tipped black, legs and feet brownish. Slightly larger and darker than *H. climacocerca* with more rufous nuchal collar, lacks white wing bands and male has longer, darker tail. *Macropsalis forcipata* is larger, darker and longer-winged, and male has much longer tail. *Uropsalis lyra* is browner and paler; male also has much longer tail. *Uropsalis segmentata* is smaller, darker and more spotted, has no nuchal collar and no obvious scapular pattern, and again male has much longer tail. Immature plumages not yet described. Race *furcifera* is larger, even longer-tailed and often paler, with paler nuchal collar. Voice. Song of male is a repetitive series of short "tsip" notes given from perches and occasionally in flight. Flight call is a high-pitched "tsig".

Habitat. Typically, forest, woodland and *cerrado*; also espinilho grassland with scattered vegetation, *campo sujo*, eucalyptus and acacia groves, urban parks and suburban parkland. Recorded at c. 500 m.

Food and Feeding. Diet includes beetles, moths, flies, mayflies, bugs, ants and Orthoptera. Foraging methods poorly studied; forages by making flycatching sallies from perches.

Breeding. Poorly known. Breeds Nov-Jan in SE Brazil; no data from other regions. Territorial. Nest-site in vegetation on rocky hillside, or among small acacias; no nest, eggs laid on bare soil or granite. Male performs courtship displays on ground, stretching and closing wings, producing wing-clapping sounds during which often rises slightly into air; also short flights during displays, wing-clapping when realighting. Clutch 2 eggs, elliptical, creamy-white, pinkish-buff or light brown, densely scrawled grey and brown; incubation and fledging periods not documented; downy chick not described.

Movements. Poorly known. Some populations may be partially migratory, e.g. race *furcifera* disappears from many areas of Rio Grande Do Sul, S Brazil, during non-breeding season.

Status and Conservation. Not globally threatened. Probably not common in Surinam and possibly restricted to S, where at N limits of range; generally rare in Paraguay, though possibly common locally in N; in Brazil, uncommon in Atlantic forest region, rare and seasonal May-Oct in Mato Grosso, common in Rio Grande Do Sul; locally common in parts of N Argentina; no data available from other regions. Disjunct population in C Peru appears to be an isolated one. Occurs in several protected areas, e.g. Noel Kempff Mercado National Park (Bolivia), Serra da Canastra and Das Emas National Parks (Brazil), Costanera Sur Ecological Reserve (Argentina).

Bibliography. dos Anjos *et al.* (1997), Barnes *et al.* (1993), Belton (1984), Brooks *et al.* (1993), Canevari *et al.* (1991), Contreras *et al.* (1990), Davis (1993), Dubs (1992), Haverschmidt & Mees (1994), Hayes (1995), Klimantis & Moschione (1987), Madroño *et al.* (1997), Miserendino (1998), Narosky, S. *et al.* (1990), Narosky, T. & Yzurieta (1993), Navas & Bo (1991), Nellar (1993), Pacheco & Whitney (1998), Parker & Goerck (1997), Parker *et al.* (1982), de la Peña (1994), Remsen & Traylor (1989), Rodríguez (1984), do Rosário (1996), Saibene *et al.* (1996), Short (1975), Sick (1993, 1997), Stotz *et al.* (1996), Teixeira (1992), de Urioste (1994), Wetmore (1926), Willis (1992).



Genus *UROPSALIS* W. deW. Miller, 1915

86. Swallow-tailed Nightjar

Uropsalis segmentata

French: Engoulevent à queue d'aronde **Spanish:** Chotacabras Golondrina
German: Schwalbenschwanz-Nachtschwalbe

Taxonomy. *Hydrosalis segmentatus* Cassin, 1849, Bogotá.
Two subspecies recognized.

Subspecies and Distribution.

U. s. segmentata (Cassin, 1849) - Colombia (W slope of Andes and E Andes) and N Ecuador.
U. s. kalinowskii (Berlepsch & Stolzmann, 1894) - C Peru (slopes of E Andes) and W & C Bolivia.



Descriptive notes. 20-22 cm (excluding outer tail feathers of male, which reach 40-7-54 cm in length); 1 male 45 g, 1 female 50 g. Sexually dimorphic. Upperparts dark brown, heavily spotted tawny, no nuchal collar; wing-coverts dark brown, spotted and barred tawny and buff, no scapular pattern; lacks white submoustachial stripe, tawny throat patch faint to absent; underparts dark brown, spotted tawny and buff, becoming tawny-buff barred brown on belly and flanks. Both sexes lack white markings on wings. Male has greatly elongated outermost tail feathers edged white, female having shorter, darker tail. Iris brown, bill blackish, legs and feet brownish.

isish. Smaller, darker and plainer than *U. lyra*, without tawny nuchal collar and throat band much reduced or absent; male has shorter tail. Smaller and plainer than *Macropsalis forcipata*, lacking buff along scapulars and tawny nuchal collar; male shows much less white in tail. Smaller, darker and plainer than *Hydrosalis torquata*, lacking buff along scapulars and tawny or buff nuchal collar; male has longer tail. Immature similar to adult. Race *kalinowskii* is similar but male has shorter tail. **VOICE.** Song of male is a whistled "purr-r-sweeee" that rises, then descends in pitch; sings from ground. Calls include low churrs.

Habitat. Typically, forest clearings, glades and openings and along forest edges, often preferring areas with bamboo, coarse grass or shrubby vegetation; recorded in humid, cloudforest and elfin forest. Also found in *páramo*, clearings along tree-line, and on open or sparsely vegetated slopes. Generally recorded at 2300-3600 m, but recent record from 1950 m on Mt Pichincha, N Ecuador.

Food and Feeding. Diet poorly studied, but probably feeds on insects. Forages by making short sallies from ground or perches. When foraging, flies low over ground, and hunts over open, grassy slopes and along forest edges.

Breeding. Very poorly known. Breeds Aug-Sept and Jan-Feb in Colombia; no data from other regions. Males perform courtship displays in which they circle and chase several females. Eggs elliptical.

Movements. None documented. Possibly sedentary.

Status and Conservation. Not globally threatened. In Colombia, considered locally uncommon to fairly common in suitable habitat; locally fairly common in suitable habitat throughout rest of Andean range. Regularly recorded in Puracé National Park, Colombia. Recently recorded from W slope of Andes in Pichincha, Ecuador, where three males were located; this area is heavily clear-cut, with frequent landslides, possibly making it more suitable for present species. No data available from other regions.

Bibliography. Butler (1979), Fjeldså & Krabbe (1990), Hilty & Brown (1986), Mazar, Kirwan & Tobias (1998), Meyer de Schauensee (1982), Olrog (1968), Parker *et al.* (1982), Remsen & Traylor (1989), Roe & Rees (1979), Stotz *et al.* (1996), Vélez & Velázquez (1998), Vuilleumier (1969), Welford (1998).

87. Lyre-tailed Nightjar

Uropsalis lyra

French: Engoulevent lyre **German:** Leierschwanz-Nachtschwalbe **Spanish:** Chotacabras Lira

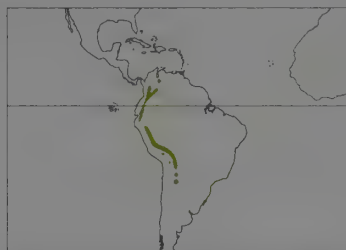
Taxonomy. *Hydrosalis lyra* Bonaparte, 1850, Bogotá.
Three subspecies recognized.

Subspecies and Distribution.

U. l. lyra (Bonaparte, 1850) - W Venezuela, W Colombia and C Ecuador.
U. l. peruana (Berlepsch & Stolzmann, 1906) - C & E Peru and W & C Bolivia.
U. l. argentina Olrog, 1975 - N Argentina and possibly S Bolivia.

Descriptive notes. 25-28 cm (excluding outer tail feathers of male, which reach 63-5-80 cm in length); 1 male 68-5 g, female 74-79 g. Sexually dimorphic. Upperparts brown, spotted greyish-white, buff, tawny and cinnamon; broad tawny or tawny-buff nuchal collar; wing-coverts brown, boldly spotted tawny and buff, no scapular pattern; tawny or buff band around lower throat; underparts brown, spotted and barred tawny, buff and cinnamon, becoming buff barred brown on flanks and lower belly. Both sexes lack white markings on wings. Male has extremely elongated outermost tail feathers tipped white; female's much shorter tail lacks white. Iris brown, bill blackish, legs and feet brownish. Smaller than *Macropsalis forcipata*, lacking buff along scapulars but with tawny or buff throat band; male has longer, darker tail. Larger, paler and more variegated than *U. segmentata*, with prominent nuchal collar and throat band; male has longer tail. Slightly paler than *Hydrosalis torquata*, and male has darker and much longer tail. Immature plumages not described. Races vary clinally in size; *peruana* is quite reddish in coloration; *argentina* has whiter markings on breast, and male's elongated outer tail feathers are tipped greyish, not white. **VOICE.** Song of male is a series of rising "wécou-tee" notes given from ground or perches. During courtship display flights, utters rapid "weep, weep, weepup"; calls include "weep, weep, weep" or "chip, chip, chip".

Habitat. Typically, humid cloudforest or rainforest, in clearings, openings and glades and along forest edges, and often near cliffs, rocky ravines or cave entrances; also open woodland, where often close to water. In Argentina, can also occur in scrub along edges of alder forest. Recorded at 800-3500 m.



Food and Feeding. Diet poorly studied, but probably feeds on insects. Foraging methods not fully described. Forages by making short sallies from ground or perches, hunting along forest edges and around clearings.

Breeding. Almost entirely undocumented. Breeds Jun-Aug and Dec in Colombia; no data from other regions. Territorial; males display to other males by hovering and flicking the elongated tail feathers to and fro, and perform courtship display flights at communal lek. No other information.

Movements. None documented. Most likely sedentary.

Status and Conservation. Not globally threatened. Local in Colombia, where recorded on Andean slopes, generally between 800-2500 m, from Valle, Antioquia, S to Cauca and Huila, and from Boyacá and Santander S to Huila; rare in Nariño, where only a few records from Pacific slope. In Ecuador, regularly recorded at Mindo, Tena and Chiriboga. In Peru, present at Tingo María. In Argentina, probably locally common in Calilegua National Park, Jujuy, where small breeding population discovered in 1997. Local throughout remainder of Andean range.

Bibliography. Boesman (1998), Butler (1979), Canevari *et al.* (1991), Chebez (1994), Fjeldså & Krabbe (1990), Fjeldså & Mayer (1996), Hilty & Brown (1986), Mazar, Pugnali & della Seta (1998), Meyer de Schauensee & Phelps (1978), Narosky & Yzurieta (1993), Olrog (1975), Parker, Bates & Cox (1992), Parker, Parker & Plenge (1982), de la Peña (1994), Remsen & Ridgely (1980), Remsen & Traylor (1983, 1989), Salaman & Gandy (1994), Stotz *et al.* (1996), Vuilleumier (1969).

Genus *MACROPSALIS* P. L. Sclater, 1866

88. Long-trained Nightjar

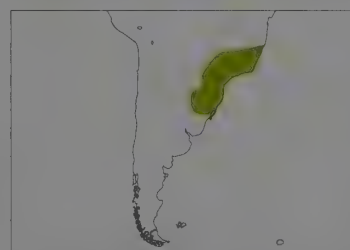
Macropsalis forcipata

French: Engoulevent à traine **Spanish:** Chotacabras Coludo
German: Hakenschwanz-Nachtschwalbe

Taxonomy. *Caprimulgus forcipatus* Nitzsch, 1840, Brazil.

Species name has commonly been given as *creagra*, but *forcipata* has priority by ten years; contrary to some claims, *forcipata* has been regularly used in literature during the past 50 years, by Brazilian ornithologists, and so should stand. Monotypic.

Distribution. SE Brazil, in Espírito Santo, Minas Gerais (possibly), Rio de Janeiro, São Paulo, Paraná, Santa Catarina (possibly) and Rio Grande do Sul; also NE Argentina (Misiones).



Descriptive notes. 28-31 cm (excluding outer tail feathers of male, which reach 48-68 cm in length). Sexually dimorphic. Upperparts brown, spotted and barred greyish-brown, tawny, buff and cinnamon; broad tawny or tawny-buff nuchal collar; lesser coverts brown, barred or spotted tawny, rest of wing-coverts brown, boldly spotted tawny and buff; shows buffish line along scapulars; no white submoustachial stripe, faint throat patch tawny; underparts brown, barred and scalloped tawny and buff, becoming buff barred brown on belly and flanks. Both sexes lack white markings on wings. Male has greatly elongated outermost

tail feathers, broadly edged whitish on inner webs; female has shorter, darker tail. Iris brown, bill blackish, legs and feet brown. Larger, darker and longer-winged than *Hydrosalis torquata*, and male has much longer tail. Larger than *Uropsalis lyra*, with well-marked scapular pattern, but throat band much fainter; male has shorter, paler tail. Larger and more variegated than *Uropsalis segmentata*, with prominent scapular pattern and nuchal collar; male shows much more white in tail. Immature plumages not described. **VOICE.** Call, given by both sexes, is a repetitive, high-pitched "tsip, tsip, tsip, tsip".

Habitat. Occurs mainly in forest and woodland, in second-growth forest, and at forest edge; in more N parts of range, tends to prefer forest in more mountainous regions. Recorded from sea-level up to 1800 m.

Food and Feeding. Diet poorly studied, but probably feeds on insects. Foraging methods poorly documented. Forages by flying close to trees and taking insects from leaves; hawks for prey in flight, and feeds on insects attracted to artificial lights; also recorded feeding from ground, beside a path, making short sallies and returning to same spot.

Breeding. Breeds possibly Nov-Jan in S Brazil; probable courtship recorded in late Sept, in NE Argentina; no data from other regions. Nest-site often shaded by vegetation, e.g. lichens and bushes; no nest, eggs laid on leaf litter on ground. Male performs courtship display on areas of bare ground, puffs out throat and raises tail at right angle to form conspicuous white V, can also hover around perched female with tail spread downwards; display areas used for up to 2 months. Eggs elliptical, pinkish-blue, speckled chestnut and buff; incubation mainly by female during day, period not known; female threatened at nest-site may perform distraction display; chick covered in greyish down, streaked buffish-chestnut and black; fledging period not known.

Movements. None documented. Possibly sedentary.

Status and Conservation. Not globally threatened. Currently considered Near-threatened. Endemic to rainforests of SE Brazil and NE Argentina. Possibly rare to locally common in SE Brazil, e.g. common in Paraná and São Paulo, rare in Rio Grande do Sul, rare in Itatiaia National Park; also present in Serra do Cipó and Serra da Canastra National Parks. Rare or perhaps very local in NE Argentina (Misiones); no data available from other regions. Throughout its limited range, habitat loss due to destruction of rainforests poses a serious threat.

Bibliography. dos Anjos *et al.* (1997), Belton (1984), Canevari *et al.* (1991), Chebez (1994), Collar & Andrew (1988), Collar *et al.* (1994), Ferguson-Lees & Faull (1992), Forrester (1993), Moraes & Krul (1995), Narosky & Yzurieta (1993), Nores & Yzurieta (1982), Olmos & Rodrigues (1990), Pacheco & Whitney (1998), Parker & Goerck (1997), de la Peña (1994), do Rosário (1996), Ruschi (1979), Santos & Krul (1995), Sick (1993, 1997), Stotz *et al.* (1996), Willis & Oniki (1981).

Genus *ELEOTHREPTUS* G. R. Gray, 1840

89. Sickle-winged Nightjar

Eleothreptus anomalus

French: Engoulevent à faucilles

Spanish: Chotacabras Pantanero

German: Sichelschwinger-Nachtschwalbe

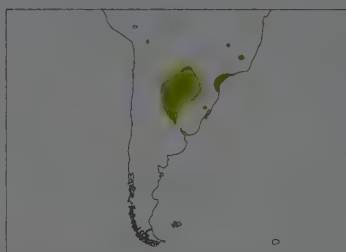
Taxonomy. *Amblypterus anomalus* Gould, 1838, São Paulo, Brazil.

Closest relative may be *Caprimulgus candicans*, which may even be congeneric (see page 305). Monotypic.

Distribution. S Brazil (Distrito Federal and Minas Gerais, patchily S to Rio Grande do Sul), C & S Paraguay (Concepción to Misiones) and N & NE Argentina (Misiones to Buenos Aires).

Descriptive notes. 18–20 cm; 1 male 43.5 g. Sexually dimorphic, with differences most readily apparent in flight. Upperparts pale greyish-brown, lightly spotted dark brown, boldly spotted blackish-brown on head; occasionally shows indistinct buffish nuchal collar; wing-coverts generally pale greyish-brown, barred blackish-brown and streaked pale buff, showing distinct cinnamon patch, distally edged whitish, on primary coverts; scapulars pale greyish-brown with irregularly shaped blackish-brown centres; pale buffish-white stripe above eye; no noticeable submoustachial stripe or white on throat; underparts darkish brown tinged cinnamon, barred brown, becoming pale buff indistinctly barred brown on lower belly and flanks. Male has distinctive wing shape with curved outer primaries tipped white and all but central tail feathers broadly tipped white or buffish-white; female browner. Iris dark brown, bill brownish or blackish, legs and feet brownish. Juvenile similar to adult female, although upperparts tinged cinnamon, especially on wing-coverts, and speckled or spotted white. **VOICE.** Calls include soft, repetitive “chip”, “tchup” or “tchut”, from ground or in flight. Flight call of female ■ harsh, nasal “gzee, gzee”.

Habitat. Edges of gallery forest, along streams or rivers through gallery forest, in monte (chaco-type woodland) or transitional woodland. In NE Argentina, recorded in grassland with areas of



chañar monte that are subject to periodic flooding. Also savanna and grassland, marshland, swamps, *campo*, scrubby edges of lagoons, and edges of streams, pools and flooded palm groves.

Food and Feeding. Diet poorly studied, but includes beetles, moths and ants. Foraging methods poorly documented. Forages in flight by fluttering and gliding low over vegetation in open country and over grassy tracks; when hunting, often rises suddenly to chase after prey.

Breeding. Poorly known. Breeds possibly Aug–Jan in SE Brazil (Aug in Paraná, Nov to early Jan in São Paulo) and Sept–Dec in NE Argentina.

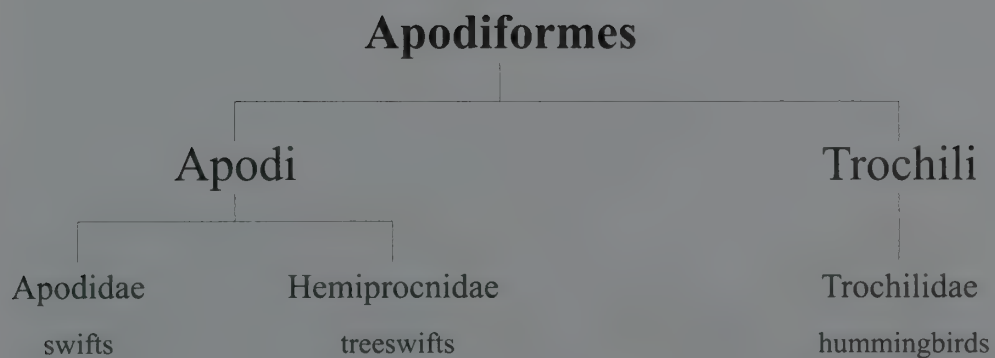
tina; no data from other regions. Territorial. Male performs courtship displays in flight, with wing-flapping sounds. Eggs elliptical or ovate, pinkish-buff or pale buffish, spotted and scrawled brown and grey; incubation and fledging periods not known; downy chick not described.

Movements. Very poorly known. May be migratory in parts of range, S populations moving N during non-breeding season, Apr–Aug.

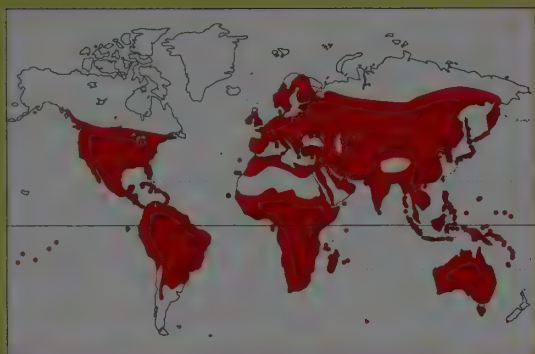
Status and Conservation. Not globally threatened. Currently considered Near-threatened. Very scarce and little known throughout range, though possibly under-recorded in many regions. In Brazil, officially protected by legislation; several protected areas, e.g. Brasília National Park, Serra da Canastra National Park and Cambuí Biological Reserve, appear to hold populations. Probably rare in Paraguay, where listed as threatened; however, recent fieldwork suggests it may be a regular inhabitant of areas of marshy grassland in E Paraguay, with apparent scarcity possibly attributable to patchy distribution and inconspicuous nature of the species; nevertheless, few definite records. In Argentina, recorded in National Parks such as El Palmar, Diamante, Pilcomayo, Mburucuyá and Iguazú, but probably a summer migrant only, moving N during austral winters. Major threat throughout range appears to be loss of habitat due to drainage, fires, cultivation, ranching, and overgrazing and trampling by livestock; also in Curitiba region of Paraná, Brazil, sand extraction and building of roads and dams, and in NE Argentina possible creation of large eucalyptus and pine plantations by forestry industry. Increasing road traffic occasionally claims some victims; collision with overhead power cables also possibly responsible for some deaths.

Bibliography. Anon. (1996f), Belton (1984), Bernardes *et al.* (1990), Bertonatti & González (1993), Borschein *et al.* (1996), Canevari *et al.* (1991), Chebez (1993a, 1994), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Contreras *et al.* (1990), Forrester (1993), Hayes (1995), López (1997), Lowen, Bartrina, Clay & Tobias (1996), Lowen, Clay *et al.* (1997), Narosky & di Giacomo (1993), Narosky & Yzurieta (1993), Pearman & Abadie (1995), de la Peña (1994), Pereyra (1939, 1950), do Rosário (1996), Ruschi (1979), Saibene *et al.* (1996), Short (1975), Sick (1993, 1997), Stotz *et al.* (1996), Straneck & Viñas (1994), Straube (1990), Wege & Long (1995).

Order APODIFORMES



Class AVES
Order APODIFORMES
Suborder APODI
Family APODIDAE (SWIFTS)



- Small to medium-sized aerial birds with long, narrow wings and short, thin legs, but strong toes with sharp claws; plumage generally rather drab.
- 9-25 cm.



- Cosmopolitan.
- Wide variety of habitats, usually not far from water.
- 19 genera, 92 species, 276 taxa.
- 6 species threatened; none extinct since 1600.

Systematics

The mainstream taxonomic view prevailing before the advent of "accessible" molecular biology was that the swifts were most closely allied to the hummingbirds (Trochilidae), with a few researchers holding out for an alliance with the nightjars and their relatives (Caprimulgiformes). Thus, the families Apodidae ("typical" swifts) and Hemiprocnidae (treeswifts) have normally been grouped along with Trochilidae in a single order, Apodiformes. In their ground-breaking work based on DNA-DNA hybridization analysis, C. G. Sibley and J. E. Ahlquist consider that, in the broadest sense, the owls (Strigiformes), the caprimulgiforms, the swifts and the hummingbirds form a monophyletic assemblage, and the traditional view that hummingbirds and swifts are close allies is further vindicated. In the arrangement proposed by these authors, the order Apodiformes, containing the families Apodidae and Hemiprocnidae, is placed with the Trochiliformes within the superorder Apodimorphae.

Divisions within the Apodidae are less certain. Two subfamilies are generally recognized. The 13 species of Cypseloidinae, comprising the genera *Cypseloides* and *Streptoprocne*, are the most ancient and least contentious: these forms do not use saliva in nest-building, and they have two carotid arteries and a primitive palate. The larger subfamily, the Apodinae, consists of three tribes. These are the Collocaliini, with the genera *Hydrochous*, *Collocalia*, *Aerodramus* and *Schoutedenapus*; the Chaeturini, containing the seven genera *Mearnsia*, *Zoonavena*, *Telecanthura*, *Rhaphidura*, *Neafrapus*, *Hirundapus* and *Chaetura*; and the Apodini, comprising *Aeronautes*, *Tachornis*, *Panyptila*, *Cypsiurus*, *Tachymarptis* and *Apus*. All members of these three tribes have a well-developed transpalatine process and one carotid artery, and all except the needletails (*Hirundapus*) use saliva in nest-building. The Chaeturini are sometimes given subfamily status as Chaeturinae. While *Schoutedenapus* is currently placed within the Collocaliini, our limited knowledge of this genus and its enigmatic members mean that its position remains far from certain.



Subdivision of the
Apodidae

[Figure: Ian Lewington]

The earliest swift-like bird, *Primapus lacki*, was described from early Eocene sediments in England and named in honour of the famous swift researcher David Lack. It was placed in the family Aegialornithidae, along with five other species described from late Eocene to Oligocene deposits in France. *Primapus* apparently died out at the end of the Eocene, although another swift genus, *Cypselavus*, described from the same French strata and originating in the Eocene, survived into the Oligocene. The Lower Eocene Green River Formation of Wyoming, USA, has yielded a small *Chaetura*-like swift, while "true swifts" of a modern genus occur in French deposits of the late Eocene (*Cypseloides mourerchauvirei*) and early Miocene (*Cypseloides ignotus*).

A. Karkhu considers that two major lineages of swift evolution can be identified and that current systematics should reflect this. First, the Paleogene, or early Eocene, taxa *Aegialornis*, *Primapus* and *Cypselavus* can be united with the genus *Hemiprocne* (modern treeswifts) in the family Hemiprocniidae. Second, the paleogenera *Procypseloides* and *Scaniacypselus*, along with the Paleogene apodiform family Jungornithidae, the Apodidae and the Trochilidae are united by the common possession of a humerus structure radically different from that of the Hemiprocniidae so defined. The first group forms Karkhu's suborder Hemiprocni, while the second, with the hummingbirds excluded, represents his suborder Apodi.

R. K. Brooke reviewed recent apodid evolution, speculating that the Cypseloidinae are the most primitive group, now restricted to a relict New World distribution, while the Apodini are the most advanced, with the Collocaliini and Chaeturini as intermediates. The rationale behind this treatment is based upon anatomical and morphological differences and the apparent development of elaborate and specialized nests and nest-sites.

Brooke's consideration of the evolution of the Chaeturini is an elegant argument based upon the degree of polytypism and patterns of distribution within New and Old World representatives of the tribe. Old World representatives are highly dissimilar, with generally fewer subspecies and disjunct distributions, as compared to their New World allies, which are very similar to one another, with a plethora of subspecies and more extensive, continuous ranges. Brooke argues that this picture suggests adaptive radiation in the New World from an "Old World stock".

The view that taxonomic conundrums within this family could be largely resolved by analysis of nest morphology has been dealt a severe blow with the realization that many species are facultative nest-builders, while a good example of the equivocal role of morphology comes from the Cypseloidinae, where it is apparent that tail spines, which were previously considered to indicate phylogeny, are in fact a function of body size and roosting habits.

The taxonomic uncertainty so prevalent in this family has its maximum expression in the swiftlets, formerly all placed in the

Swifts are well known as being amongst the most aerial of all birds. In common with several other bird families they regularly feed on the wing, but, much more remarkably, it is thought that they sometimes actually copulate in mid-air, although this is certainly very difficult to prove. They are also extraordinary in the habit of aerial roosting; to date this has been convincingly demonstrated for only one species, the Common Swift, which has been seen to collide with aircraft while roosting high in the sky. Popular belief has it that they fly faster than any other birds, but this is probably something of an exaggeration, although there is no doubt that their normal flight is fast. The structure of the wing is clearly visible in this Common Swift. Note the long, narrow primaries and the very short secondaries, an arrangement which facilitates fast flight and efficient gliding.

[*Apus apus apus*,
Surrey, England.
Photo: Kim Taylor/
Bruce Coleman]





This Pacific Swift shows several morphological features of interest in the Apodidae, such as the sharp claws. Of particular note is the large eye, which is typically sunk back into the face, with a patch of dark, bristle-like feathering in front of it. These feathers can be moved by muscles in order to adapt to the angle of incidence of the sun's rays, and they almost certainly help to reduce glare, which could otherwise be a major problem for birds that spend much of their lives flying around in direct sunlight.

[*Apus pacificus pacificus*, Paluma, Queensland, Australia.
Photo: Clifford & Dawn Frith]

genus *Collocalia*, and which J. L. Peters described as one of the most difficult of all groups of birds. As recently as 1970, Brooke split *Collocalia* into three groups: *Hydrochous*, containing the large waterfall-dwelling Waterfall Swift (*Hydrochous gigas*); *Collocalia*, containing glossy, non-echolocating species; and *Aerodramus*, containing non-glossy species, including echolocating taxa. This proposal is supported by recent studies of phylogeny within the Collocaliini, and specifically of the correlation between phylogeny and behaviour. These studies concluded that comparisons of cytochrome *b* sequences strongly suggest that the Collocaliini are not monophyletic, although "evidence in support of a Collocaliini clade is provided by ectoparasitic lice...*Collocalia*, *Aerodramus*, and *Hydrochous* are all parasitized by the louse subgenus *Collodemyus* (genus: *Dennyus*), which is found in no other host". The researchers also noted that there was no evidence of consistency between nest-building behaviour and their molecular phylogeny, whereas echolocation showed better agreement. A holistic approach to taxonomy in this group, and the family as a whole, using molecular data, morphology and biology, will no doubt give a clearer picture of many of these issues.

Very recently, in 1998, J. Holmgren presented a parsimonious phylogenetic tree for the Apodiformes, "consistent with a hypothetical historical narrative and zoogeographical facts". This placed *Schoutedenapus* in the tribe Apodini and included the treeswifts as a tribe Hemiprocnini within the Apodinae. Holmgren suggested that, at a higher taxonomic level, behavioural characters might reveal an evolutionary conservatism in the swifts not unlike that found in the swallows and martins (*Hirundinidae*). Unsurprisingly, however, he concluded that all taxa should be fully analysed, using all available techniques, before any real consensus could be established.

Morphological Aspects

As anyone examining a swift would agree, both the genus name *Apus*, from the Greek *a-pous*, meaning "without foot", and the former name for the order, *Machrochires*, "with large hands" (referring to the outer wing), are well chosen.

The swift wing, when compared with those of other bird families, is instantly recognizable by its nine or ten long primaries and

its compressed block of eight to eleven very short secondaries. Remarkably, the longest primary can measure up to three times the length of the shortest secondary, compared with only twice the length in the evolutionarily convergent *Hirundinidae*. This is a function of the very long carpometacarpus, which considerably exceeds the length of the radius and ulna. Both the primaries and the secondaries produce a powerful forward force, with the primaries providing an additional downward force, while lift is produced mainly in the secondaries. This configuration gives members of this family great speed. The Chimney Swift (*Chaetura pelagica*) was among the fastest of 12 species monitored for flight speed using Doppler radar, while swiftlets entering cave breeding sites have been recorded flying at up to 111 km per hour. Various speeds much greater than this have been claimed for a number of larger species: notably, White-throated Needletails (*Hirundapus caudacutus*) have allegedly been recorded flying at 170 km per hour. The uniquely long and narrow wing shape is advantageous during flapping flight, but actually favours gliding, and this may explain the low flight-metabolism figures recorded for swifts. In addition, the tendency to glide reduces the need for powerful breast muscles, as shown by the figures for breast/body weight of 15.5% and 19.5% for Alpine Swifts (*Tachymarpis melba*) and Pallid Swifts (*Apus pallidus*) respectively, as compared with 26.5% for the pigeons (*Columbidae*), a group of typical flapping birds.

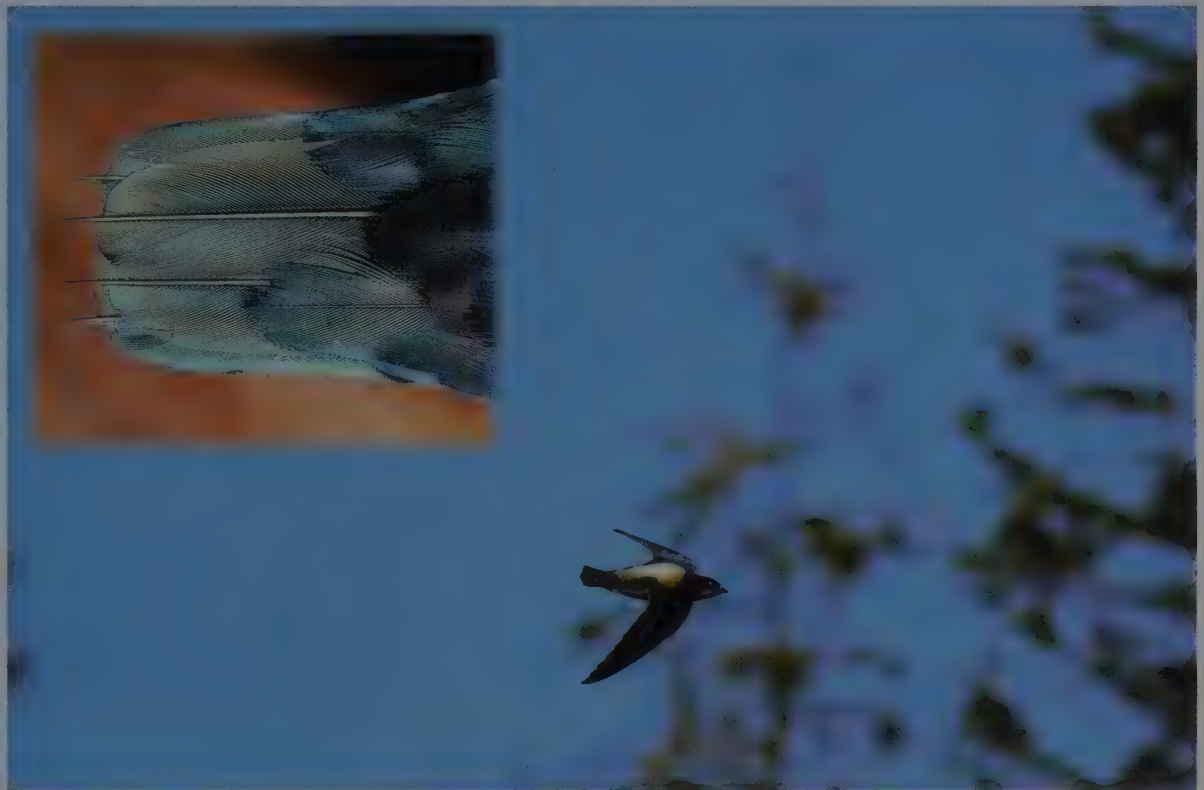
Swifts normally have ten rectrices, although there is a remarkable example of polyrectricity, a Common Swift (*Apus apus*) with 12 rectrices, but beyond this the general form of the tail is highly variable. A tail fork is a prominent feature of many Apodini, while the tails of swiftlets have only shallow furcation. Several species have an enhanced tail fork resulting from deep emargination and extension of the outer rectrices; this is most apparent in the genera *Panyptila*, *Tachornis* and *Cypsiurus*. In the tribe Chaeturini, and to a lesser extent in the Cypseloidinae, the rectrix rachides extend beyond the feather tips, causing the distinctive "spines" or "needles" after which many of these species are named. They are analogous with the stiffened tails of woodpeckers (*Picidae*) and treecreepers (*Certhiidae*), serving to support the birds when they alight on vertical surfaces. Some species within the Chaeturini have a remarkably short tail, notably the Neotropical Short-tailed Swift (*Chaetura brachyura*) and the Afrotropical Böhm's Spinetail (*Neafrapus boehmi*). This short-

Members of the Chaeturini, like these White-throated Needletails, are characterized by the unusual structure of the tail feathers, with the rachides bare at the tips and stiffened along their whole length, both of which features combine to help the birds cling to vertical surfaces. They are amongst the glossiest of all swifts, and it is interesting to speculate on possible aerodynamic functions of both the glossy plumage and the "spiny" tails.

[*Hirundapus caudacutus*
caudacutus,
Daclin, Heilongjiang,
China.

Photo: Roland Seitre/Bios.

Inset: *Hirundapus*
caudacutus caudacutus,
Queensland, Australia.
Photo: Dave Watts/
ANT/NHPA]



fall in the tail is perhaps countered by a distinctive broadening of the secondaries, which probably enhances manoeuvrability.

The tiny feet of swifts belie their effectiveness. Anyone who has handled these birds will be aware of the strength of their feet and the sharpness of their curved claws. These features, together with calluses on the tarsi and stiff tail feathers, are essential for gripping onto vertical surfaces, though the feet are generally useless for perching. All but one of the swifts have four toes, the sole exception being the Papuan Swiftlet (*Aerodramus papuensis*), which has three, having lost the hallux, or hind toe. In an important revision of the literature on the arrangement of the toes in swifts, C. T. Collins noted that the Chaeturini and the Cypseloidinae possess a typical anisodactyl foot, with the hallux directed backwards and the second, third and fourth toes directed forwards; the Collocaliini also share this feature. At the same time, he revised views of the much-vaunted pamprodactyly in the Apodinae. This arrangement, with all toes pointing forwards, is commonly exhibited in museum specimens, but living birds adopt it only when the toes fail to gain purchase, as on a smooth, hard surface. In the typical grasping formation, the first and second toes (the hallux and innermost) are spread medially, together or slightly apart, and oppose toes 3 and 4 (the central and outermost), which are spread laterally. This arrangement is also shown by chameleons (*Chamaeleo*) and phalangeroid mammals such as the koala (*Phascolarctos cinereus*), a situation which appears to represent, as Collins states, "a particularly clear but overlooked case of convergence among these three classes of climbing vertebrates".

Evidence from blood-testing shows profound physiological adaptation to a high-altitude way of life. The haemoglobin is sensitized for optimum delivery of oxygen in conditions of low oxygen pressure. Erythrocyte dimensions are generally greater than in other bird families, facilitating exchange of oxygen, and oxygen affinities are significantly higher than those recorded in passerines.

The gape is very large, facilitating the aerial capture of insects, although the bill itself is quite tiny. The eyes of all species of swift are protected by coarse, bristle-like feathers located immediately in front of the eye; the angle of these feathers can be altered by muscles. These "bristles" are black, and this, coupled with the deeply recessed position of the eyes, suggests that they may also play a role in reducing glare directly onto the eye. Swifts are far-sighted and focus both monoptically and bioptically. They

have both central and lateral foveae. One species, the Spot-fronted Swift (*Cypseloides cherriei*), has particularly large eyes which account for an astonishingly high proportion (5.5%) of its body mass. It is also thought that this species, like its congener the White-chinned Swift (*Cypseloides cryptus*), may be able to use very basic echolocation.

Echolocation is highly developed in a number of swiftlet species. Unlike bats (Chiroptera), however, swiftlets do not apparently have the echolocating acuity needed to home in on insect prey. Rather, this facility gives them the advantage of being able to nest in dark cave sites, as well as to feed later into the evening than non-echolocating species, so that they can return to their caves after dark. The work of Lord Medway and J. D. Pye showed that the echolocating group of swiftlets might be diphyletic, with the majority uttering a double orientation click, while the Atiu Swiftlet (*Aerodramus sawtelli*) and the race *lowi* (at least) of the Black-nest Swiftlet (*Aerodramus maximus*) utter single clicks. These differences were believed to be the result of anatomical modifications, but our poor understanding of the mechanism that produces these sounds greatly restricts speculation and led these two researchers to conclude that it would be preferable to place all echolocating swiftlets in a single genus. C. T. Collins and R. Murphy considered that "a well developed kinesthetic or spatial memory would seem to be a necessary supplement to the echolocation capacities of swiftlets".

A distinguishing feature of all members of the subfamily Apodinae, except probably the needletails, is the use of saliva as a binding mechanism for nesting material. In the Edible-nest Swiftlet (*Aerodramus fuciphagus*) this is taken to extremes, saliva being used for the construction of the whole nest. In the breeding season, the sublingual glands of both sexes are greatly enlarged to facilitate the production of large amounts of this "nest-cement". This salivary glue is composed largely of glycoproteins, and holds remarkable properties that make it attractive to the human world in various ways (see Relationship with Man).

The plumages of all swifts are certainly dull, although there are exceptions to the black or brown theme. In two closely related Neotropical species, the Chestnut-collared Swift (*Cypseloides rutilus*) and the Tepui Swift (*Cypseloides phelpsi*), all adult males and some adult females have a bright chestnut-reddish throat. Many species are decidedly glossy in plumage. This reaches its extreme

in certain members of the Chaeturini, most notably the Philippine Spinetail (*Mearnsia picina*), the Purple Needletail (*Hirundapus celebensis*) and the White-throated Needletail, and also in the Collocaliini in the aptly named Glossy Swiftlet (*Collocalia esculenta*). One form of the last of these, *amethystina* from Waigeo Island, has brilliantly dark violet-blue upperparts. Nearly all swifts, however, show at least a slight gloss in fresh plumage. It is hard to determine the function of these feather glosses, although it is interesting to note that they are exhibited also by most hirundines. Perhaps the increased albedo of glossy feathers is important in protecting the plumage, which is so constantly exposed to direct light during aerial foraging, or could it be that the gloss has some effect on thermoregulation or aerodynamics?

In many migratory species, moult is completed on the wintering grounds, after migration. In some species, it starts before the onset of migration and is then suspended during migration, being completed on arrival in the tropics. Perhaps the most remarkable fact relating to the moult of swifts comes from the Common Swift, and presumably applies to other temperate-breeding species as well. After fledging, juvenile Common Swifts do not undergo a complete moult until their second winter in Africa; as a result, their remiges will be used for one and a half years before being replaced. In addition, moulting Common Swifts do not always replace the outermost primary on each wing, and therefore these feathers might not be replaced for up to two and a half years. When moult is recommenced in such individuals, second-winter or otherwise, it commences with the outermost primary.

Some swifts, notably in the genus *Chaetura*, moult during the breeding season. Studies of breeding Vaux's Swifts (*Chaetura vauxi*) show that moult strategies are individually variable. Some Vaux's Swifts in Oregon, USA, were recorded using communal roosts for part of each day in August and September, presumably while building up their reserves for migration and continuing their moult. The Chimney Swift finishes its primary moult by early October, while in the first stages of its migration.

Resident species may wait until the end of the breeding season before moulting, although some species of swiftlet that have extended breeding seasons employ similarly drawn-out moult strategies. The White-throated Swift (*Aeronautes saxatalis*) is unusual among migratory species in that it moults during the breeding

season, perhaps because in its relatively northern wintering grounds the period of peak food abundance is over before the swift arrives.

Habitat

Swifts are highly specialized feeders and breeders, requiring foraging areas with adequate concentrations of aerial plankton, while at the same time needing ease of access to their particular breeding and roosting sites. These two habitat characteristics are sometimes exclusive of one another and require that daily movements, on various scales, be undertaken. Those species that lay relatively large clutches, and whose chicks therefore have the most rapid growth rates, need to forage closest to the nest, while those with smaller clutches and slower rates of growth can forage at greater distances. Thus, for swifts generally, and for the former group in particular, the concept of nesting habitat is often restricted to the immediate vicinity of the nest-site (see Breeding), since the vulnerability of all swifts when not on the wing has led to nest-site security, especially inaccessibility to terrestrial predators, being of prime concern.

Swift habitat in its simplest expression is a site where prey can be taken. For many species, this means regular journeys well away from the breeding or roosting area. This is less of a problem for the large species than for the smaller ones. In the cordilleras of northern Venezuela, around the famous Henri Pittier National Park, the large and rapidly moving White-collared Swift (*Streptoprocne zonaris*) is able to utilize the wide range of habitats available within several kilometres of the highlands where it nests and roosts. When rain falls in the highlands, these swifts will move into the adjacent lowlands to feed, even foraging at building height over the streets of nearby cities.

The well-studied Common Swift has perhaps the most catholic habitat preferences of any swift. In the breeding season it is found from north-west Africa and the Middle East north to Arctic parts of Scandinavia and Russia, and sweeping east to the Pacific. Across this enormous breeding range it occurs in such disparate habitats as desert, Mediterranean scrub, steppe, farmland, suburbia and the centres of great cities. Wintering in sub-Saharan Africa, it can be seen over any habitat, even including forest, which is shunned by many swifts. This species, feeding from rooftop level to great



Plumage coloration is particularly drab amongst the Apodidae, and almost all species are covered in varying tones of blackish, dark brown or paler dull brown, sometimes with bluish or greenish gloss. Apart from two *Cypseloides* species with rufous throats and collars, the overall dark colouring is punctuated only by areas of white or whitish, most typically on the throat or rump, but sometimes elsewhere on the underparts, or on the forehead. The White-throated Swift has rather extensive white on its underparts, and is notable in showing a distinctive white trailing edge to the wing, most heavily marked on the secondaries.

[*Aeronautes saxatalis*
saxatalis,
western Montana, USA.
Photo: Alan G. Nelson/
Animals Animals]

Having channeled their evolutionary energies towards success in a highly aerial lifestyle, swifts are not adept at moving about on the ground. Nevertheless, their small feet are surprisingly strong and, with the sharp claws, are well designed to help the birds perch on vertical surfaces, though they are not suitable for grasping horizontal branches.

When clinging to a steep rock face, like this Alpine Swift, or to a vertical wall, like this Common Swift, the birds often use the tail to gain greater purchase, as also occurs in some tree-climbing families of bird, such as the woodpeckers (Picidae), woodcreepers (Dendrocolaptidae) and treecreepers (Certhiidae).

Indeed, members of the spintail tribe, Chaeturini, show a similar modification of the tail feathers as is to be found in these families, although swifts do not clamber about the surface in the same way, tending simply to stay put where they are perched. Swifts' clumsiness in moving about on the ground would make them ideal targets for terrestrial predators, which explains their habit of perching in such inaccessible sites. Visible on these two birds is the round-headed, broad-faced appearance, brought about in part by the birds' wide gape, which helps in their aerial foraging for insects, though the bill itself is short and rather weak-looking.

[Above: *Tachymarptis melba melba*, Göreme, Turkey.
Photo: Alfred Limbrunner.

Below: *Apus apus apus*, Mörfelden, Hessen, Germany.
Photo: Ingo Arndt/
Bruce Coleman]



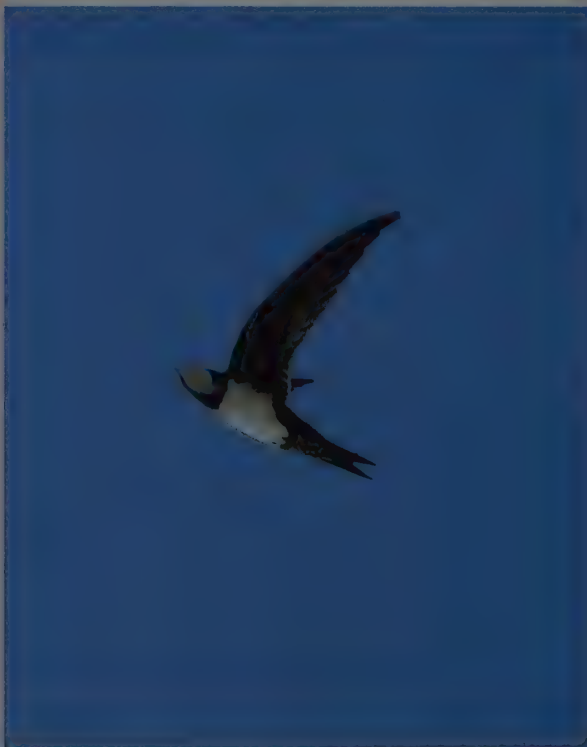
heights, typifies above all others the adaptive success of the family. If the food supply is adequate and suitable nesting sites exist, it will breed; and if adverse weather causes a temporary lack of suitable food, it will travel long distances to avoid such conditions before returning to its nest (see Movements).

Water is an important requirement for all life, but it is fundamental in the breeding cycle of many insect species. As a consequence, swifts are seldom found far from it. This is especially evident with species such as the Pallid and White-throated Swifts which penetrate arid interior habitats. The former is found around many oases in the central Sahara, while the latter, although breeding in the arid south-central USA and northern Mexico, always has meadowland, typically damp, within easy reach of its nesting sites. Water reaches its maximum prominence in the habitats of the largely waterfall-dependent New World Cypseloidinae and the South-east Asian Waterfall Swift. Again, however, both of these taxa occur over a great range of habitats adjacent to their secure roosting and breeding sites and presumably benefit from, among other things, the ease with which nesting materials such as liverworts and mosses can be gathered.

Some species have more specific habitat requirements. The palm-dependent genera *Cypsiurus* and *Tachornis* are seldom found far from their arboreal hosts, and the charismatic Böhm's Spintail is often found near baobabs (*Adansonia digitata*). Some swifts occur exclusively in and around forest and have shown little ability to adapt to the fragmentation of this habitat. The classic example must be Sabine's Spintail (*Rhaphidura sabini*), with its near-continuous distribution in the West African forest belt and relict East African outposts such as the forest of Kakamega in west Kenya.

General Habits

No group of birds is so fundamentally adapted to an aerial existence as the Apodidae. This has a profound effect upon all aspects of their lives.



Although superficially similar to the swallows and martins (Hirundinidae), and long associated with them in classifications, swifts belong to a quite different branch within the avian tree, and most of the similarities can be put down to convergent evolution for a highly aerial lifestyle. Most swifts can readily be distinguished by their long, narrow wings, which are swept back like sickles, and which indeed slash through the air to similar effect. It is perhaps the swifts' dashing style of flight which best separates them from the hirundinids. The White-rumped, Pallid, Pacific and Alpine Swifts all show slight variations on the "typical-swift" silhouette of the Apodini.

[Above left:
Apus caffer,
Wakkerstroom, Transvaal,
South Africa.
Photo: Warwick Tarboton.

Above right:
Apus pallidus pallidus,
Ras Al Khabbah, Oman.
Photo: Hanne &
Jens Eriksen.

Below left:
Apus pacificus pacificus,
Yakutsk, Siberia.
Photo: Bill Coster/NHPA.

Below right:
Tachymarpis melba
melba, Kavala, Greece.
Photo: Alfred Limbrunner]

Most swifts are highly gregarious throughout the year, frequently exploiting short-term concentrations of food. They often form large mixed flocks with other swift species and other aerial feeders, primarily hirundines. Resource-partitioning occurs within such mixed feeding flocks as a result of size-specific and perhaps taxon-specific preferences in diet.

Exploitation of the aerial feeding space is clearly of great importance in flocking behaviour, but it also confers other advantages. Several raptor species regularly take swifts, not least some falcons (Falconidae). In North America White-throated Swifts are often caught by Peregrine Falcons (*Falco peregrinus*), while in the south-western Cape, South Africa, Little Swifts (*Apus affinis*)

accounted for 19% of 121 prey items taken by Eurasian Hobbies (*Falco subbuteo*). Even the large and powerful Alpine Swift has been taken by the Sooty Falcon (*Falco concolor*), while swiftlets are commonly included in the diet of Bat Hawks (*Macheiramphus alcinus*), which have been persecuted as a consequence, due to the economic importance of the swiftlets (see Relationship with Man). Swifts frequently mob small raptors while emitting alarm calls and undertaking rapid evasive movements.

The Common Swift also forms large flocks before migration, although actual migration is typically undertaken in smaller groups. Non-breeding and breeding birds leave colonies at the same time. Indeed, the cohesion of the colony may sometimes

Waterfalls are favoured by several apodids, such as the Great Dusky Swift. Some species are merely seen foraging in the vicinity, but others roost and nest beside the falls or actually behind the curtain of water.

When admiring the awe-inspiring power of the relentless cascades of water, it seems scarcely conceivable that such small birds should take such risks, but it would appear that they seldom come to harm, although there are rare records of birds being washed downstream. Nevertheless, if there is a rapid increase in water flow during the breeding season, the birds are sometimes unable to reach their nests.

[*Cypseloides senex*,
Falls of Iguazú, Argentina.
Photo: Michael Fogden/
DRK]



transcend species boundaries, as screaming parties from mixed colonies of Common and Pallid Swifts appear to be directed at groups of swifts from other, "rival" colonies.

At night most swifts rest, although parents at the nest continue to incubate their eggs or brood their young. Chattering can be heard all night from the colonies of certain species, and it is likely that no swifts are "heavy sleepers". Resident populations often roost at the nesting site, and swiftlets of several species spend the whole year roosting in or close to their nests. A good deal of roosting behaviour is, however, gregarious and use of roosts is not confined to those adults and their young that have used the site for breeding. One chimney nest-site of Vaux's Swifts contained a post-breeding roost of 16 birds, of which only one of 11 young present had been fledged at the site. Interestingly, D. Lack's classic Oxford study suggested that young Common Swifts did not return to the nest after fledging. However, fledglings of several species will return to roost at the nest with the adults, and in some species to rest during the day, for up to a week after their first flights.

The celebrated aerial roosting of swifts has been proved, with certainty, only for the Common Swift. It may also be practised by Pallid and Alpine Swifts, since these species, like the Common Swift, have exceptionally refined oxygen-collecting ability; this results from concentrations of haemoglobin surpassed only by hummingbirds and akin to those found in montane species living at over 2500 m. On the breeding grounds, aerial roosting is particularly frequent in first-year birds and typically involves occupation of the airspace at an elevation of 1000-2000 m, though roosting to 3000 m has been recorded. Aerial-roosting flocks initially involve screaming parties, which become close-circling, rapidly rising groups. In western Europe, this behaviour occurs in late evening in the warmest weather from the end of May; in periods of bad weather, roosting by non-breeders in potential nest-sites has been noted. As the breeding season progresses, breeding adults may also be found in the aerial-roosting flocks. Some newly fledged individuals are also believed to roost in this manner. Altitude is maintained by slow wingbeats with intermittent gliding, typically flying into the wind, which provides lift. This behaviour may prove to be frequent throughout the year. The Common Swift will also roost on walls, in tree hollows, on tree trunks or even on the outer foliage.

The length of the roosting period is subject to a number of variables. These can be broadly grouped as climatic, such as light

intensity and temperature, and therefore geographical location; age-related; and behavioural, including breeding and migratory status. All these factors are ultimately related to food supply and energetics.

Swifts are relatively late risers from terrestrial roosting sites, presumably owing to the diurnal pattern of prey density. The most northerly Common Swift populations roost longer after sunrise (which occurs earlier) than do those farther south. Equally, better weather brings an earlier start to the day's activities than poor weather, while birds with young roost later than those without young, presumably to take advantage of maximal prey densities while conserving adult fitness. Prior to their migration, temperate species extend the length of this "lie-in". Little Swifts are mainly early and late feeders and spend much of each day in pairs at their nests, to some extent presumably sheltering from the hottest period of the day. In this species, roosting time is photosensitive, with birds from poorly lit colonies roosting on average 10-13 minutes later than those from well-lit colonies.

The roosting behaviour of Chimney Swifts studied in Illinois, USA, has also been proved to be influenced by climatic variables. Swifts stayed in the roost-site longer and re-entered it earlier on cold or rainy days, and those with low wind turbulence. All these environmental variables affect the abundance of aerial insects. On average, these swifts left their communal nesting chimneys 11 minutes before sunrise in flocks of 70 birds, and re-entered the roost 20 minutes after sunset in flocks with a mean of 83 birds. The roosts consisted mainly of non-breeders, with up to 300 in a single chimney. One site in Portland, Oregon (USA), holds an autumn roost of Vaux's Swifts that numbers an estimated 20,000-30,000 individuals. Such pre-migratory roosts may help with conservation of fat reserves and even moult in some species. Indeed, it has been observed that Chimney Swifts can increase their body weight by up to 51% prior to autumn migration.

A pair of White-chinned Swifts has been observed roosting, the partners side by side, in the constant spray of a waterfall close to a nest. White-collared Swifts roost in similar situations, invariably attempting to stop others of their species from roosting near them by raising one or both wings, depending on whether both pair-members are present, to prevent "intruders" from landing. Perhaps the most intriguing roosting behaviour observed by M. Marín and F. G. Stiles, in their study of Cypseloidinae species, involved a pair of Spot-fronted Swifts one of which clung



Great Dusky Swifts typically nest on horizontal ledges close to a waterfall, or sometimes actually behind it. This choice of nest-site clearly gives the birds considerable protection from predators. Here hundreds of birds can be seen clinging, almost bat-like to the damp rock faces between two branches of the waterfall, their pale heads appearing white from a distance. The swifts also roost around waterfalls, again presumably for protection, and during the day they make feeding forays out over the canopy of the forest nearby. The Great Dusky Swift is locally common in suitable sites, from the lowlands to about 1000 m, mainly in Argentina, Brazil and Bolivia, and it may also occur in Peru and, more rarely, in Paraguay. It may be threatened in places by dam building along some of its rivers.

[*Cypseloides senex*,
Falls of Iguazú, Argentina.
Photo: Günter Ziesler]



Clustering close together and clinging on to the rock face with their sharp claws, these Great Dusky Swifts are protected from the direct spray by an overhang in the rock. Nests located at such sites are virtually impregnable to any potential predators. There tend to be plenty of mosses and liverworts nearby, and these the swifts collect to construct their nests. The nest itself, made of soft plant matter and stuck together with saliva, is usually built at the top of a cleft in the rock. It is a raised structure, exposed to the daylight, an unusual case amongst the Apodidae. The adults do not appear to mind being moistened by the spray of the waterfalls, but the nestlings are protected from chilling in these humid sites by a thick coat of down.

[Above:

Cypseloides senex,
Falls of Iguazú, Argentina.
Photo: Günter Ziesler.

Below:

Cypseloides senex,
Falls of Iguazú, Brazil.
Photo: Kevin Schaffer]



to a tiny ledge of rock, its wings hanging loosely, while its mate was "clinging to the shoulder or upper back of the first, with its tail also fully spread bracing it against the first"!

In particularly cold weather, swifts employ a number of warmth-saving strategies. Roosting pairs of Common Swifts ruffle their feathers, arch the back and often roost one on top of the other. Huddled groups have been noted in several species. Non-breeding Alpine Swifts roost on the outside wall of colonies, forming dense writhing clusters in response to cold weather. A flock of migrating Chimney Swifts roosting on the trunks of two palm trees formed a dense layer, with individuals touching, though not on top of each other as was the case in an open noc-

turnal roost of migrating Vaux's Swifts, when the air temperature was 25°C.

Radio-tracking technology has been used to investigate the roosting habits of wintering White-throated Needletails. One was tracked back to a low strip of sclerophyll woodland in the Gongiberoo Range, Australia, where it probably roosted in a hollow tree. Such sites are likely to be traditional, and this bird returned to the same place, with other needletails, on consecutive nights.

During unusually bad weather, swifts may form daytime roosts, presumably to rest and conserve heat. A particularly impressive instance was recorded after a period of cold weather in Morocco, when three dense clusters of Alpine Swifts, totalling some 350 individuals, were found clinging to a sheltered part of the city wall in Fez.

It has also been established that the White-throated Swift and, from available evidence, almost certainly the White-throated Needletail, too, can enter a torpid state similar to that well documented for certain nightjars, most famously the Common Poorwill (*Phalaenoptilus nuttallii*) of North America (see page 309). The needletail's temperature was recorded dropping from 38.5°C to 28°C, only 3°C above ambient, over two hours during the night, and in the morning it returned rapidly to 38°C in just a few minutes. Strongly variable body temperature has also been recorded in other swifts. Further data may prove such a phenomenon to be widespread in the family.

Roosting in mixed-species assemblages has been recorded, and is particularly common among the Cypseloidinae at waterfall sites. Furthermore, the Chimney Swift is one of several North American species from a variety of families that apparently occur in the roosts of Common Starlings (*Sturnus vulgaris*) and Common Grackles (*Quiscalus quiscula*).

Many aerial displays have been studied but, as R. B. Fischer observed in the 1950's, most swift displays, being aerial, appear destined to remain poorly understood. Fischer's work on Chimney Swifts revealed that aerial displays were affected by precipitation and, in particular, low temperatures; cessation of display as a result of such climatic conditions is most likely to occur early in the season. In his studies of Chimney Swift display, he recognized two distinct phases which he called "Early" and "Later". The former began when the swifts returned for the summer, flying in loose associations of 4-7 individuals without feed-

ing. Pairs would often break from these larger groups and fly together. Speculation suggested that this behaviour was in preparation for the synchronized behaviour which would ensure breeding success later. The second phase is characterized by "trio-flying", in which two males chase a female between various physical obstructions, all three birds constantly calling loudly. These flights may exceed five minutes in duration and at their peak may involve ascents to 150 m at increasing distance from the nearest nest-site. Rarely, one of the pursuing males will physically attack the other. One feature of this display is a sharp chipping call that was initially believed to be produced by the female, although later observations seemed to contradict this. However, it is interesting to speculate that, as with the Common Swift, a sexual shift in the tone of the call may exist in the Chimney Swift, thereby accounting for this apparent difference.

Various similar chasing displays are a feature of the behaviour of many swifts. Paired Short-tailed Swifts fly parallel to each other with extravagantly slow wingbeats while slowly uttering ticking notes, and White-collared, White-chinned and Chestnut-collared Swifts have been observed performing chasing displays similar to those documented for Chimney Swifts. A presumed female White-collared Swift was chased by up to three males before rejoining larger flocks. During chases, a posture known as "V-ing", with both wings held high above the body, may occur in power dives. Fischer also recognized a V-ing display when the following individual in a pair suddenly snaps into position; this may or may not be performed by the leading bird, too. It can be noted in trio-flying, but not during hot pursuit. This behaviour reaches its greatest expression in established pairs. Many other species produce similar displays. In Common Swifts the procedure is more pronounced, and is often repeated several times, the wings meeting over the back and producing an audible clap before being rapidly lowered beneath the body to meet again.

Communal screaming by fast-moving flocks rushing around the area of the colony is a familiar feature of a number of *Apus* species. In Common Swifts these displays are most frequent in the evening, though by no means restricted to this period, and often involve the whole colony, with individuals in nest-holes joining in the calling and often leaving their nests to participate.

The display is typically initiated by a single calling individual rapidly approaching the colony. It can take only a few seconds but consists of five or six circuits and be repeated quickly several times in succession. Before migration, these displays sometimes involve individuals from several colonies.

In this family, both the nests and the individual birds play host to a wide variety of invertebrate parasites. In Africa, the main species are hippoboscids flies (*Crataerina*, *Pseudolynchia*, *Ornithomya*), feather-lice (*Dennyus*, *Eureum*) and ticks (*Lelaptidae*, *Proctophyllodidae*, *Analgesidae*, *Eustathiidae*). Some of these swift parasites are endemic to particular groups, suggesting a considerable degree of co-evolution. As anyone who has handled swifts can testify, heavy parasitic infestations are not uncommon. The reasons for the unusually heavy parasite loads carried by this family may be related to preening difficulties caused by extreme anatomical adaptation to an aerial way of life.

Voice

Swifts are very vocal. Their calls are most frequently given during the breeding season, when the greatest variety can be heard. Although the calls of most swifts are superficially similar, recent studies have given researchers important insights into aspects of their behaviour and taxonomy.

This is nowhere more apparent than in the case of the high-pitched screaming of the Common Swift, such a familiar sound in Europe, where it typifies the summer to ornithologists and the general public alike. The excellent study of E. Kaiser has revealed that males utter a "ree" scream and females a high-pitched "swee". It has long been known that the pair-members duet to produce the distinctive "swee-ree" call, but Kaiser's work has enabled him to solve many behavioural problems. For instance, the screaming of non-breeding birds outside nest-holes which they are prospecting allows occupants to indicate that both of the pair are present; if the prospector still chooses to enter the nest, it will be attacked by the same-sex member of the pair. This clearly has implications for a whole range of breeding issues, and most importantly for pair formation. Kaiser has speculated that further research will show that



Swifts are in general highly gregarious in most of their activities, regularly foraging, nesting and roosting in the company of conspecifics. One of the species most famous for its communal roosts is Vaux's Swift, and at one roost-site in Portland, Oregon (USA), an estimated 20,000-30,000 birds gather together every autumn, using the site for several weeks at a time. The birds shown here, at a Mexican site, were part of a large group of Vaux's Swifts roosting in a well cut into the limestone bedrock.

[*Chaetura vauxi gaumeri*, Cozumel Island, Mexico. Photo: Robert Behrstock]

The Mottled Spinetail is particularly closely associated with baobab (*Adansonia digitata*) trees in dry woodland, although it can be seen in a range of woodland types. It normally roosts in baobabs, typically in groups of 5-11 birds, though over 100 birds have been recorded at such a site in Angola. The birds seen here were roosting inside a huge baobab tree of great antiquity, estimated as being some 2500 years old.

[*Telecanthura ussheri benguellensis*, Gona-re-zhou Game Reserve, Zimbabwe. Photo: Mark Homann]



all other species in the family can be sexed using call, at least those that are sexually monochromatic or that nest in the dark.

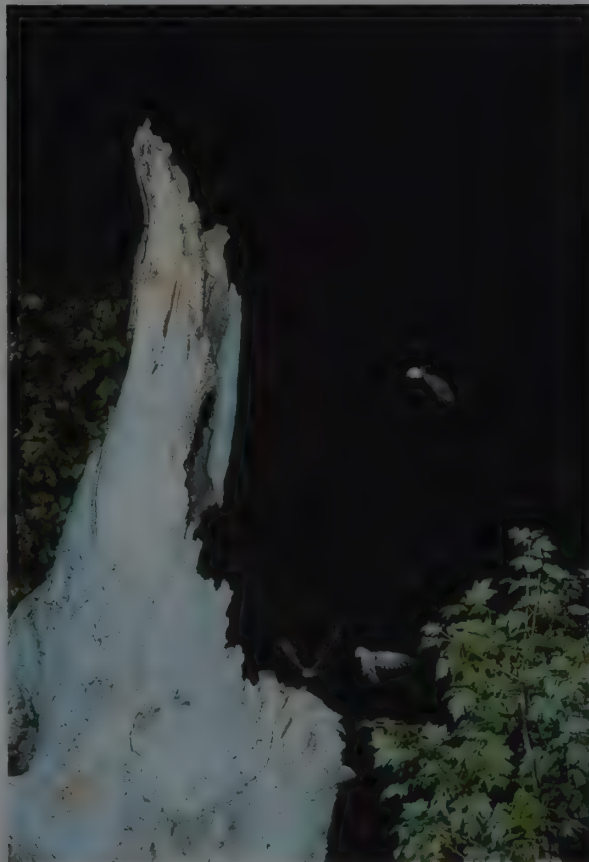
Perhaps the most fascinating of all vocal adaptations are the echolocating calls of certain swiftlets. These calls, which are paralleled only in the Neotropical Oilbird (*Steatornis caripensis*), were studied in a series of experiments by Medway and Pye (see Morphological Aspects). The echolocating calls of swiftlets are within the human spectrum of hearing and are harsh trills that accelerate and decelerate; they have been likened to running one's finger across the teeth of a comb. Unlike bats, echolocating

swiftlets lack the acuity to feed on insects using echolocation alone, and sight remains their primary sense for capturing prey. Echolocation does, however, enable swiftlets to navigate within deep cave systems and perhaps to feed later into the evening than other aerial bird species. It is possible that this has helped them to compete in a niche typically occupied by free-tailed bats (*Molossidae*), as this family of bats is poorly represented in those areas of the tropics where the swiftlets are present.

Two species in the Cypseloidinae, the White-chinned and Spot-fronted Swifts, have been recorded uttering calls that may have

As their common name suggests, Chimney Swifts are famed for nesting and roosting in chimneys, but they will also use natural sites, as here, where the birds are returning to roost in the hollow bole of a broken beech tree; it is nowadays rare to find this species nesting in such a site. Research has shown that the weather conditions can have a significant effect on the birds' behaviour at their roost. On cold or damp days, they tend to remain in the roost-site longer in the morning, and return to it earlier in the evening, probably in connection with fluctuations in the abundance of the aerial insects they feed on.

[*Chaetura pelagica*, Ohio, USA. Photos: S. Maslowski/FLPA]





The White-collared Swift is found from Mexico south to Brazil and Bolivia. Within this extensive range, it occurs in a fair variety of habitats from sea-level up to over 4000 m, from the coast up into the mountains. It generally nests in damp caves, typically behind waterfalls, where it may breed alongside Great Dusky Swifts (*Cypseloides senex*). The nest is a small pad of mud and plant material, with mosses and liverworts. In many areas breeding begins late in the dry season, timed so that the young are in the nest at a time when the insect supply is plentiful early in the wet season.

[*Streptoprocne zonaris bouchellii*,
River Tiribí, Costa Rica.
Photo: Manuel Marín]

echolocating implications. The poorly studied Scarce Swift (*Schoutedenapus myoptilus*) has also been noted as having a call resembling that of the swiftlets, and it is tempting to speculate that echolocation ability may extend beyond that group. When one considers the crepuscular feeding and cave-dwelling habits, both actual and analogous, of many swift species, the high-frequency, high-pitched trills of most swifts cry out for further examination.

Sounds akin to the drumming of snipes (*Gallinago*), produced by allowing certain feathers to vibrate, have been recorded in the Apodidae. Male Common Swifts have been noted producing brief "trrr...t" sounds while V-ing after aerial copulation, while Mottled Swifts (*Tachymarptis aequatorialis*) have been observed spreading the tail and moving it horizontally until the outer rectrix nearly touched the wing, where it vibrated, making a loud "prrrpt-prrrpt-prrrpt". This occurred while the birds were diving to the surface of a reservoir to drink.

Food and Feeding

All swifts feed exclusively on insects and spiders, taken mainly in the air. Their diets have been studied by analyses of stomach contents, droppings, pellets or food boluses, and all methods have revealed the importance of Hymenoptera (bees, wasps, ants), Diptera (true flies), Hemiptera (true bugs) and Coleoptera (beetles). Stinging insects are generally avoided, while mimics of stinging insects are taken. Work in Zaire has shown that Common Swifts feed almost entirely on stingless honeybee drones when foraging around hives. Nevertheless, an Alpine Swift was found, when examined, to have a number of stings lodged in its throat.

It has been suggested that smaller swifts typically take a greater variety of relatively small prey, while larger swifts tend to consume a larger number of a few species. This is due in no small part to the ability of larger species to take particular advan-

tage of swarming insects as a result of their extensive foraging areas, which may allow them to exploit a number of climatic zones in a short period of time. Indeed, this ability has led to a specialization among larger species generally to exploit concentrations of single species of insect. For instance, 800 winged ants were recorded in the stomach of a Venezuelan White-collared Swift, and 681 fire ants (*Solenopsis geminata*) were found in a single White-naped Swift (*Streptoprocne semicollaris*). Smaller swifts also feed on swarming insects, however, and data from prey analyses of many smaller species show that they will take advantage of temporarily bountiful prey sources. It is their more limited foraging ranges that reduce their consumption of such prey. These limited ranges reflect the need to stay close to larger clutches and comparatively many rapidly growing nestlings that require frequent feeding; in many of the larger swifts, with fewer, slowly growing offspring, the converse is true.

White-collared Swifts exploit the food sources disturbed by seasonal fires in South America. Even more opportunistic feeding behaviour was noted in southern Africa by W. R. J. Dean, who was followed for over 50 minutes by up to three Alpine Swifts; these caught cicadas (*Cicadidae*) that he flushed from around him as he walked through shrubland. White-throated Swifts have been noted following a combine harvester, apparently taking disturbed insects.

Although all swifts are selective with regard to both prey size and prey species, their gape size, which is essentially dependent on absolute size, remains a limiting factor. This helps reduce interspecific competition in much the same way as aerial stratification does in mixed flocks. The difficulty of comparing the diet of one species with that of another is confounded by geographical variation in diet. In north-west Italy, Pallid Swifts have been shown to take smaller prey with a greater number of dipterans and hymenopterans compared with Common Swifts, which took more aphids and coleopterans. At Gibraltar, on the other hand, Pallid Swifts have been noted taking significantly larger prey than

The swiftlets, comprising the genera *Hydrochous*, *Collocalia* and *Aerodramus*, form an assemblage of small, very similar, rather nondescript species. The taxonomy of this group is very confused, with uncertainty and dispute at generic, specific and subspecific levels. The forms currently split off into the genus *Aerodramus*, including the Australian Swiftlet, are amongst the drabest of the lot, but they are certainly not the least interesting. These are the famous cave-nesting forms that navigate amidst the gloom of their caves by means of echolocation, uttering a stream of metallic clicks as they fly. Their feats of navigation in the dark are all the more remarkable because the birds nest in sizeable colonies, with many nests clustered together in a small area, so that not only do the birds have to steer clear of the cave walls and projecting outcrops, but they must also avoid all of their neighbours flying busily around the nests. Australian Swiftlets breed in caves, or between large boulders or in gorges, where they typically form dense colonies.

[*Aerodramus terraereginae*
terraereginae,
coastal north-eastern
Queensland, Australia.
Photo: G. Anderson/
ANT/NHPA]



Common Swifts. One study of Pallid Swifts in Morocco revealed a relatively high proportion of spiders, although it has been suggested that this might have been just a manifestation of the comparatively brief period over which samples were collected.

Seasonal prey differences may also prove to be acute in some species, though a Costa Rican study showed that there was no significant difference between the types of prey taken by Band-rumped Swifts (*Chaetura spinicauda*) in the wet season and those taken in the dry season. Bolus-content analysis in Common Swifts indicates that the decline of mass insect swarmings at the end of the breeding season leads to a sharp fall in the numbers of many nutritious insect species within the birds' foraging airspace, and to a subsequent increase in the number of beetles taken. Differences between the diets of adults and nestlings may also contribute to seasonal variations in prey taken.

A radio-tagging study of the breeding-season diet of Vaux's Swifts revealed that the adults foraged up to 5.4 km from their nests, primarily over land, with water used less frequently. Perhaps surprisingly, no variation in diet was recorded between the five study sites or during the course of the day. The 233 boluses examined contained the astonishing total of 24,133 spiders and insects.

Generally, the larger the swift is, the smaller the number of prey items it takes, with a corresponding increase in prey size. The Common Swift averages about 300-500 prey items per bolus, compared with 156-220 in the larger Alpine Swift. Studies of prey size in three *Cypseloides* swifts showed that most of the prey taken by the Spot-fronted Swift, the smallest species, was 1-4 mm long, compared with a general range of 8-11 mm for the Black Swift (*Cypseloides niger*), the largest species. Interestingly, the intermediate species, the White-chinned Swift, showed a bimodal pattern, with peaks of 41.3% of prey items in the 4-5 mm range and 38.4% around 11 mm long.

The above examples show that swifts, far from being the random "vacuum cleaners" of folk biology, are actually exact selectors of prey. Indeed, White-collared Swifts have been observed to be particularly choosy when feeding on leaf-cutter ant queens, as they discard the thin cephalothorax in the process of cutting off the fat abdomen. Many species swallow such indigestible elements and expel them as pellets. Several studies comparing the diets of swift species in areas where traps have been used to sample the insect fauna have found that the different species' diets do not translate exactly into the composition of insect life available.

Although most swifts lack the high manoeuvrability of hirundines, some do feed close to the canopy. In perhaps the greatest divergence from typical apodid foraging, hovering Papuan Spinetails (*Mearnsia novaeguineae*), Grey-rumped Swifts (*Chaetura cinereiventris*) and Chimney Swifts have been noted apparently taking food from foliage, and it has been suggested

that such behaviour may be more common and widespread within the family than is currently suspected. A flock of Chimney Swifts was seen feeding by diving basically tail-first through openings in the upper storey of a tree, in the manner in which they enter chimneys, fluttering briefly and gleaning insects from leaves lower down the canopy. Even more surprisingly, an individual of that species was once recorded apparently attempting to take a dragonfly (Odonata) from a Purple Martin (*Progne subis*), which was trying to position the insect in its mouth before swallowing it.

The Glossy Swiftlet has been shown to be as manoeuvrable as sympatric hirundines, allowing it to feed very close to the tree canopy. Its diet has been found to contain a larger proportion of homopterans and coleopterans than those of other tropical swifts, its foraging technique giving access to prey items that are generally unavailable to these other species. Even caterpillars have featured in the Glossy Swiftlet's diet.

Most swift species feed significantly higher than tree-top level, although, at least in Europe, the reduction in insect numbers above 100 m enforces a typical upper limit. Competition among various swift species, and with other aerial feeders, is generally avoided by differentiation in prey size and also by selection of different altitudinal strata. A study in Ecuador showed that, when similar species were foraging within the same column of air, the larger ones would occupy the higher strata. Similar results were obtained from Niah caves in Sarawak, where there was vertical stratification of three swiftlet species, and to some extent from Kariba in Zimbabwe, where the larger species generally fed in the higher strata.

Feeding is often concentrated during certain times of the day. For example, the Waterfall Swift is predominantly a crepuscular feeder, and several cave-dwelling species apparently feed late into the evening, thanks to their echolocating abilities (see Voice). Little Swifts tend to rest in the heat of the day (see General Habits), feeding both earlier and later. Truly nocturnal feeding has been recorded for the Alpine Swift and the Indian Swiftlet (*Aerodramus unicolor*), both of which have been seen exploiting the food source from around lights, while Alpine Swifts may apparently feed in total darkness. It is possible that nocturnal feeding is more widespread in the family than is currently thought.

Swifts drink regularly, by dropping to the surface of a body of water and dipping in the lower mandible. Surprisingly small areas of water are used for this purpose. Insects are also taken from the water's surface.

Breeding

Swifts generally pair for long periods and are apparently monogamous. A study of Pallid Swifts in Italy showed that mate



The fact that swifts are so aerially orientated and comparatively inexpert on the ground means that drinking, like many other activities, is performed on the wing, as demonstrated by this White-throated Needletail. A bird will skim down low over a stretch of water and dip its head to take a mouthful while in full flight, before rising up and often returning to repeat the process several times.

[*Hirundapus caudacutus*, Daclin, Heilongjiang, China.
Photos: Roland Seitre/Bios]



Swiftlets typically breed in large, densely packed colonies, with a great many nests clustered close together, as in this colony of Glossy Swiftlets in northern Borneo. Unlike those swiftlets placed in the genus *Aerodramus*, this widespread and common species apparently has no ability to echolocate, which is consistent with its general avoidance of the dark interiors of caves, its favoured nest-sites including cave entrances, cliff overhangs, hollow trees, and also buildings, always in places where there is sufficient daylight. In this species, each nest is a small cup made of a mixture of small roots, mosses and lichens, glued tightly to a vertical surface using the birds' saliva.

In contrast to these habits, many members of *Aerodramus* commonly nest in partial or total darkness, where they navigate by means of echolocation. Also, many make extensive use of saliva in forming the actual nest itself, and in some cases nests may even be constructed exclusively of saliva. Such nests are the most highly valued for the multi-million-dollar bird's-nest-soup business, a trade which has had serious impact on swiftlet populations in many areas.

[*Collocalia esculenta*
cyanoptila,
Sabah, Borneo.
Photo: Jean-Paul Ferrero/
Ardea]



Many swifts have adapted their ancestral habits to take advantage of the relatively new nest-sites available in man's constructions. Thus, some nest under the eaves of bridges, while many occupy suitable sites under the roofs of houses. This is the case of the Little Swift and also of its eastern counterpart, the House Swift (*Apus nipalensis*), which may actually be conspecific. These species form small, rather untidy agglomerations of bag-like nests constructed mainly of grass and feathers, cemented together with saliva, each with a small tunnel or slit as its entrance.

[*Apus affinis affinis*, Masai Mara National Park, Kenya.

Photo: Derek Bromhall/Oxford Scientific Films]

and nest-site fidelity were much lower than recorded for other European swifts. The advantage gained by the ability of faithful pairs to nest earlier than non-faithful pairs was, however, insufficient to manifest itself in significantly different breeding success. Paired individuals of many tropical species may stay together all year round, and some swiftlets are known to roost in pairs at the nest-site throughout the year. In the case of migrant species, bonds must be renewed annually. Among Common Swifts, for example, partners remain together throughout the tenancy of a nest-hole. Pair-bonding starts with non-breeding first-summer birds, which will go so far as to occupy a nest-site and build a nest, which they will defend in subsequent years.

For all swifts, the breeding season is related, primarily, to the abundance of insect life. This simple fact has a great impact on breeding biology. In the tropics it means that breeding coincides with the wet season, while in temperate zones summer breeding is invariably the rule. The length of time available for breeding has a profound effect on many aspects of breeding biology. Seasons are shorter for species that breed in the highest latitudes than for those breeding in climates which can support adequate insect populations for longer periods. For example, the Common Swift has a single clutch, while the more southerly Pallid Swift can produce two clutches. Production of two clutches is commonest in the tropics and has been reported for a number of species. In the case of the wide-ranging Little Swift, distinct breeding seasons are generally recorded in areas with the most marked seasonality, whereas in some equatorial regions year-round breeding can occur.

Studies of swiftlets breeding in the vast limestone caverns of Niah, in Sarawak, indicated that even in seemingly seasonless equatorial climates variations in the timing of breeding occur. Although the majority of Black-nest and Mossy-nest Swiftlets (*Aerodramus salangana*) breed between September and April, some breed throughout the year, as the climate is never too harsh. Glossy Swiftlets have three seasons within a year, and it was speculated that varying day-length might serve as a regulating mechanism. Observations of the number of swiftlets returning to and leaving from the caves suggested a degree of variation in food supply through the year, not least during the monsoon, when persistent downpours cause frequent prey shortages.

Although the broadly similar breeding seasons of the Black-nest and Mossy-nest Swiftlets suggest very similar biologies, the

former feeds at higher elevations than the latter and would perhaps be more likely to suffer from comparatively irregular food supplies. The Black-nest Swiftlet shows a number of adaptations to this dietary dilemma. Both the single egg and the hatchling can withstand long periods without brooding, with consequent temperature reductions, and the fledging period is protracted; in addition, both adults and juveniles can tolerate periods of relative starvation.

For the genus *Cypseloides*, the wet season brings not only abundant food, but also nesting material and suitable conditions for it to adhere to a substrate. Nesting therefore starts anything from one to three months after the beginning of the wet season. In the related genus *Streptoprocne*, the White-collared Swift begins laying late in the dry season, so that the young benefit from early wet-season insect abundance. On Penang, off the west coast of the Malay Peninsula, the Edible-nest Swiftlet's breeding season appears to show a very limited relationship with rainfall, suggesting a fairly constant supply of insect prey; indeed, the majority of eggs hatch in the dry season.

Swifts utilize a wide range of nest-sites. Most are in dark places, and many swifts in fact nest in pitch-black conditions. This is nowhere more apparent than in the echolocating swiftlets, which use their most distinctive sensory attribute to fly considerable distances into the total darkness of some cave systems. Although Common and Pallid Swifts generally choose holes as the safest type of nest-site, the eaves of buildings are often preferred, and the usage of sites probably varies with local availability. Nowadays the Common Swift nests almost exclusively in man-made structures.

Most species have precise nesting requirements. These have been investigated in great detail for the North American Black Swift, and they indicate why some swifts are often absent from what appears to be suitable habitat. Studies have revealed six constant features: water; inaccessibility; darkness; unobstructed flyways immediately in front of the nest; rock niches on which to build; and usually high relief. Clear access to the nest entrance is an important feature for many species. For example, the African Palm-swift (*Cypsiurus parvus*) has been found to require a flyway of 40 m; and the Mottled Swift nests only in dry granite sites with at least 6 m of clear airspace in approach, except in caves.

Other swifts depend in intriguing ways upon various bird and plant species. Horus Swifts (*Apus horus*) nest in colonies of bee-

Sitting still on its nest, this Spot-fronted Swift blends remarkably well into its surroundings, despite the highly distinctive white patches on its head; indeed, these too almost appear to imitate the background substrate, as a form of disruptive camouflage. This species typically nests in wet sites close to a waterfall, and, as here, the outside of the nest itself may be permanently wet. Favoured sites are rocky ledges with some protection offered by an overhang. The nest is plastered with mosses and liverworts on the outside, while the inside of the cup itself is normally lined with leaves or fern fronds.

[*Cypseloides cherriei*,
River Tiribí, Costa Rica.
Photo: Manuel Marin]



eaters (Meropidae), kingfishers (Alcedinidae) and martins (Hirundinidae), while White-rumped Swifts (*Apus caffer*), and in some areas House Swifts (*Apus nipalensis*), use old nests of Red-rumped Swallows (*Hirundo daurica*). Both New World (*Tachornis*) and Old World (*Cypsiurus*) palm-swifts depend on various palm species. Indeed, the distributions of some of these swifts have increased as the result of an initial range expansion by some of their "host" species. The relationship between the White-rumped Swift and various hirundines is clearly one of antiquity, as Red-breasted Swallows (*Hirundo semirufa*) rarely breed in sites higher than 1 m above ground-level, thus avoiding nest parasitism by the swift; this implies a form of evolutionary "arms race". Perhaps most fascinating of all is the close correlation in the Californian range of Vaux's Swift with that of the Pileated Woodpecker (*Dryocopus pileatus*), the swift nesting in the roosting cavities of the woodpecker. It has even been suggested that Pileated Woodpeckers provide the majority of this swift's nest-sites.

The most typical nest construction is a self-supporting bracket, often attached to a vertical wall. Most swifts use saliva to hold nest materials together and to fix the nest to the substrate. The relatively immense amount of saliva required is produced in the sublingual salivary glands, which are enlarged in the breeding season (see Morphological Aspects).

There are several exceptions to the bracket-shaped nest. The two species of the genus *Panyptila*, the Great Swallow-tailed (*Panyptila sanctihieronymi*) and Lesser Swallow-tailed Swifts (*Panyptila cayennensis*), diverge greatly from this blueprint. Both species incorporate plant down into the nest-wall matrix, using saliva, to produce a material that is typically likened to felt. They make tube-like constructions, that of the larger species measuring up to 66 cm in length, which either hang from their base or are attached along their whole length to a vertical surface.

The three New World palm-swifts, the Antillean Palm-swift (*Tachornis phoenicobia*), Pygmy Swift (*Tachornis furcata*) and Fork-tailed Palm-swift (*Tachornis squamata*), site their nests on the outward-facing surfaces of dried palm fronds. The interior nest-wall is covered in downy seed cases, while the outer wall consists mainly of an untidy covering of loose feathers. The Old World equivalent of these three is the genus *Cypsiurus*, comprising the Asian (*Cypsiurus balasienensis*) and African Palm-swifts. Their nests are similarly, though more openly, constructed and

are typically placed on the upper surface of a palm frond. Both seem more adaptable than their New World cousins, since they have also taken to nesting close to the trunks of some palms, or on thatched roofs and other man-made structures.

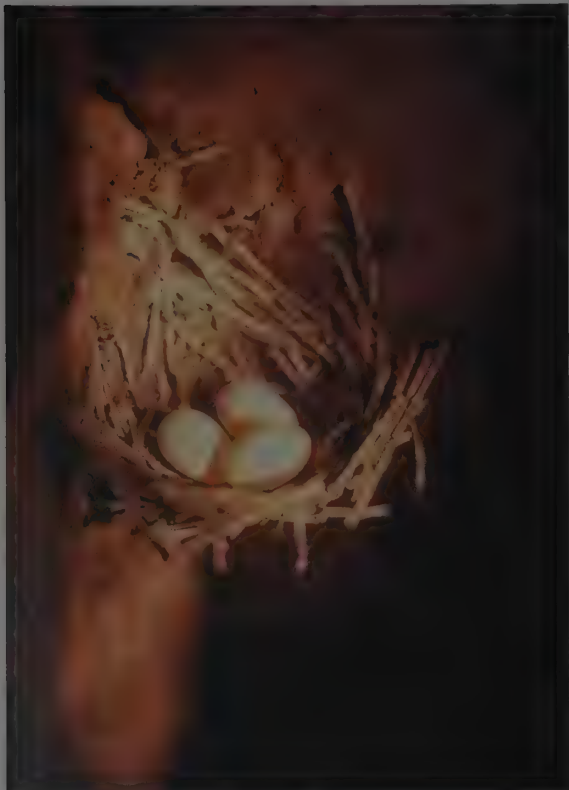
The Cypseloidinae, and probably also the needletails, are unusual within the family in not using saliva in nest construction. Four large tropical species do not always build nests, but instead use unlined scrapes in the nest-site substrate. These are the New World White-collared and White-naped Swifts and the Old World Brown-backed (*Hirundapus giganteus*) and White-throated Needletails, and the same probably applies also to the other two, less studied *Hirundapus* species. The New World pair, however, will sometimes make nests, depending upon the circumstances of the site, and it has been suggested that further research into the needletails will reveal similar facultative tendencies.

Saliva reaches its maximum usage in swiftlet nests, and in one species in particular, the Edible-nest Swiftlet, the nest is con-

The Chestnut-collared Swift nests close to water, in shady sites near waterfalls, and sometimes in sea caves. Its nest is a neat cup-shaped structure, built mainly from mosses and liverworts, and attached by its mud base to a rock ledge. The usual clutch is of two eggs, which are incubated for about 25 days. Additional dry plant matter can be added to the lining while the nest is in use.

[*Cypseloides rutilus*
brunitorques,
River Tiribí, Costa Rica.
Photo: Manuel Marin]





structured entirely of saliva. The African Palm-swift uses saliva to glue its eggs to the nest, as these are laid in a comparatively exposed position. After laying an egg, with her body pressed firmly against the nest flange, the female slips down over the egg until it is in contact with her breast, at which point she makes a retching action, places her head alongside the egg and applies saliva on the nest next to the egg. A similar process may occur in the Fork-tailed Palm-swift.

An assortment of vegetable matter is used to form the basis of many nests. This is typically collected from airborne detritus and is carried to the nest-site in the bill, though some species have been noted taking material from the outer branches of trees, using their feet. Various cypseloidine species have been observed clinging to water-splashed rock walls and collecting mosses and liverworts for use in nest construction. Nesting materials are frequently stolen from other birds, including other swifts of the same species.

Common Swifts defend their nest-sites, often tenaciously. Potential intruders will call from outside a nesting cavity to ascertain whether or not it is occupied. Entry may induce a conflict, which could carry on for hours and even be fatal. Recent studies into sexual differences in calls indicate that prospecting swifts can glean information regarding not only the occupancy of a nest-site but also whether a pair-bond has been formed, all without entering the nest.

Fighting occurs only after a threat display: one bird approaches the other, both wings raised and one tipped slightly to one side, exposing the strong feet; the relatively feeble bill is used only rarely, and then to little effect. Initial pair reunions invoke threat displays, although mutual preening occurs on reformation. Subsequent returns to the nest by one or other of the pair will elicit a greeting display which is believed to be a mild version of the full threat display. Similar displays are recorded for many other species. In the threat display of the Spot-fronted Swift, both the wings and the body are raised.

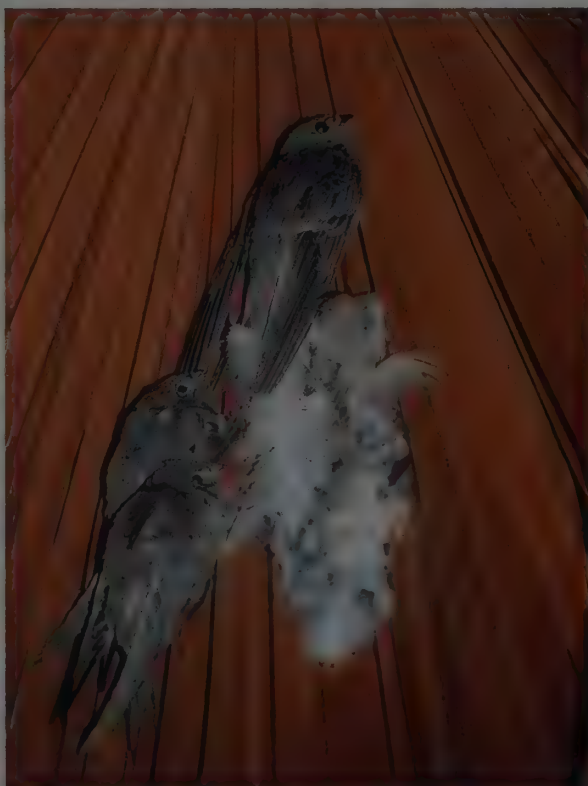
Aggression can be aimed at other species competing for the same nest-sites. Common Swifts invariably win these contests when faced with House Sparrows (*Passer domesticus*), though they are less successful against Common Starlings. The most dramatic conflicts involve Alpine Swifts and Feral Pigeons, the domesticated form of the Rock Dove (*Columba livia*). These last two species often breed peaceably alongside each other, but in one instance two adult Alpine Swifts were recorded attacking an airborne pigeon by attaching themselves to it, one on top and one beneath, and flying it directly into a pavement, causing the pigeon serious injury. Aggressive behaviour towards a variety of species has been noted close to colonies: for example, the Plain Swift (*Apus unicorn*) has been observed mobbing Northern House-martins (*Delichon urbica*), and several

Böhm's Spinetail is an Afrotropical swift with very specific habitat requirements, being associated particularly with baobab trees.

The nest seen here was situated in the heart of a large baobab, deep inside a vertical cavity. Access to this cavity was through a hole some 50 cm in diameter at the top of the trunk. The nest was constructed mainly from leaf petioles, and was sited about 5 m below the entrance hole, where it was in near-darkness.

This particular nest site is known to have been used in successive years. *Böhm's Spinetail* has also been recorded as nesting in deep man-made pits.

[*Neafrapus boehmi* sheppardi, Pafuri, South Africa. Photo: Warwick Tarboton]



Several swift species are closely associated with palm trees, most notably those of Old World *Cypsiurus* and New World *Tachornis*, all of which regularly nest in palms. The African Palm-swift normally nests in rather a confined space, but it requires a clear approach route of some 40 m so that it can fly in close to the ground, and then swoop sharply upwards into the leaves. The nest itself, attached vertically to the side of a leaf, is made mainly of feathers, moulded into a small cup to cradle the eggs, which in turn are glued to it using the birds' adhesive saliva.

[Left: *Cypsiurus parvus myochrous*, Nylstroom, Transvaal, South Africa. Photo: Warwick Tarboton.

Right: *Cypsiurus parvus myochrous*, Marondera, Zimbabwe. Photo: Peter Ginn]

In the Black-nest Swiftlet, both sexes brood their chick, apparently relieving each other always at night. Sometimes the hatchling is left alone for a while, during which time its temperature naturally drops, but it appears to be adapted to withstand such treatment. The Black-nest Swiftlet is a colonial cave-nester, and is one of several swiftlet species whose nests are collected as a delicacy in Chinese cuisine, an activity with a long tradition, but which is now threatening a number of species. The dark nest of this species has a high proportion of translucent saliva, mixed with feathers, and is one of the nests most sought after by the traders.

[*Aerodramus maximus lowi*,
Gomantong Caves,
Sabah, Borneo.
Photo: Roland Seitre/Bios]



individuals of this same swift species combined to chase away a much larger Alpine Swift.

Aerial displays (see General Habits) precede apparent aerial copulation. Some observers are sceptical as to whether this most famous of swift behavioural adaptations does actually occur, and conclusive proof would clearly be very hard to come by. What is thought to be aerial mating has been recorded for a number of species in several genera. In Common Swifts, the female flies in front of the male with her wings held close to the vertical, causing a forward plunge; the male rapidly follows and, as the female levels out into a horizontal flight on quivering wings, he will attempt, often unsuccessfully, to mount her, his wings held high and straight while hers are horizontal, in a shallow gliding descent. More rapid, steeper descents are not uncommon, and this display can occur without apparent mating. One impressive variation on this theme has been recorded for the American White-throated Swift, in which pair-members fly directly towards each other, unite and then "pin-wheel" towards the ground for several seconds.

In South Africa, in late October, M. van Gelder watched two African Palm-swifts tumbling out of the same palm 22 times during 30 minutes, "locked together and spiralling like a winged seed". Although on one occasion he thought that he could see cloacal contact, he was not certain whether this behaviour was copulation or territorial confrontation. Each time, the birds broke from physical contact just above the ground, and then circled back into the palm fronds to start again. A third bird was in close attendance on three occasions, though van Gelder was certain that the tumbling always involved the same two birds. A week later, he noticed that a nest was being built in this particular palm tree. He remarked that, if this had been aggressive territorial behaviour, it seemed strange that the adversaries had co-operated to the extent of not falling to the ground.

Scepticism as to whether these aerial contacts do involve copulation is intensified by the knowledge that the Common Swift is also recorded mating at the nest, as are many other species. Some species, for example many of the swiftlets, are thought to mate only at the nest. M. Marín and F. G. Stiles speculate that

aerial copulation could involve a greater risk of failure, and therefore infertility of eggs, which would certainly be disadvantageous for species which lay small clutches.

Within the apodid family, egg colour is uniform: dull white, seemingly without exception. The eggs of Alexander's Swift (*Apus alexandri*), resident in the Cape Verde Islands, were originally described as white, finely freckled red-brown, but this was apparently based on a misidentification. Swift eggs are relatively small, but have a high yolk content. They vary in size from about 15.5 x 10 mm in the Fork-tailed Palm-swift to 43 x 28.5 mm in the White-collared Swift. Clutch size varies considerably, from a single egg in some swiftlets to seven or more in some *Chaetura* and *Hirundapus* species. The role of both clutch size and egg size is important in responses to unpredictable weather. It has been shown that egg formation in Common Swifts is sensitized to weather-related fluctuations in insect abundance, since females have difficulty in accumulating sufficient energy reserves during poor weather. Larger, older nestlings outcompete younger siblings. Egg size correlates well with nestling survival, as chicks from larger eggs fledge more quickly than those from small eggs, and it has been speculated that size variation in eggs within a clutch is an adaptive strategy serving to optimize sibling competition, facilitating brood reduction in times of inclement weather.

In all species that have been studied in detail, the two sexes share equally in nesting duties. This is presumably another adaptation to the variability of food supply. The inability so far shown by various swift species successfully to raise artificially increased broods shows that nestling survival is finely balanced, and that breeding can place considerable cost upon the adults. According to the model presented by J. Maynard-Smith, such a situation of shared responsibilities evolves when two parents can raise twice as many fledglings as one would have been able to, or when the chance of a deserting parent re-mating is small.

The work of M. J. Tarburton at Chillagoe, in Queensland, revealed a unique incubation strategy. The Australian Swiftlet (*Aerodramus terraereginae*) lays two clutches per season, each of one egg. The second egg is laid 50 days after the first, and is incubated by the developing chick from the first clutch. The



Young swifts hatch naked and in most species they remain so until the flight and contour feathers start to appear, only a very few species growing an interim covering of downy feathers. These Common Swift nestlings are only a day or two old, and their eyes are still closed, but the first signs of the incipient feather tracts are clearly visible on the back of the right-hand chick. The young are fed on a rich diet of insects, which are brought back by the adult in the form of a bolus, and regurgitated directly into the throat of the hungry nestling. If necessary, Common Swift nestlings are able to survive for weeks with very little food, partly by their laying down layers of fat when food is plentiful.

[*Apus apus apus*,
Oxfordshire, England.
Photo: Derek Bromhall/
Oxford Scientific Films]

chick's incubating posture is identical to that of the adult and is apparently stimulated by the presence of the egg, although, given the cramped conditions within the nest, there may be little option for alternative behaviour. The nestling incubated the egg throughout the day and probably during the night, despite the adult being present at the nest. The chick's brood patch is also closely similar to that of the parent. There was no significant difference between the incubation periods for the first and second eggs, indicating similar levels of efficiency for the two strategies. In those nests where the first nestling fledged before the second egg hatched, incubation of the latter was completed by the adults. Laying of the second egg, however, is generally timed so that it does not hatch before the first chick fledges. It has been estimated that this strategy saves over three weeks in the total length of the breeding season. Among the intriguing questions raised by this discovery is the possibility, as yet unknown, of hormonal changes in the nestling of the kind associated with incubation in adults. This strategy is considered to be an extreme adaptation to the limited and variable food supply at Chillagoe. All swifts have relatively long nestling periods, again an adaptation to a capricious supply of food. The brooding of the second clutch by the nestling of the first allows swiftlets at Chillagoe nearly to match the annual production of White-rumped Swiftlets (*Aerodramus spodiopygius*) in relatively food-bounteous Fiji.

Large, or rapidly laid, clutches recorded in three *Chaetura* swifts and the White-rumped Swiftlet have been attributed to more than one female laying in the same nest. In one of these species, the Chimney Swift, extra-parental co-operation has long been proven. A third adult, presumed not to be a parent, was observed to be sharing a nest-site and participating in some nestling duties such as feeding, which it performed more frequently than the parents, and brooding. R. W. Dexter's study showed that three adults at a nest was typical, although four were recorded in six out of 22 cases. The additional birds were often first-years, perhaps even the young of the occupying adults from the previous season; in other cases they were very old adults. Helpers were more often males than females. Some of these

scenarios were maintained for more than one season. What seems at first sight an example of apodid altruism is probably a behavioural mechanism benefiting the helper as much as the brood and parents. Helpers are typically first-year birds that would not be able to breed successfully and so do not defend a nest-site; they therefore require a secure roosting site. By undertaking certain nesting responsibilities they are allowed access to a safe roosting environment. As Dexter speculated, some of these visitors are probably just awaiting an opportunity to obtain a mate.

Clutch size in tropical swiftlets has been discussed at length by Tarburton, and it has some general implications for the whole family. Comparison between Australian and White-rumped Swiftlets suggests that food reliability and quantity determine clutch size. In Tarburton's two-year study there were very different levels of rainfall. In the dry year, when there were fewer insects available, the feeding rate was reduced, while in the wet year, with more insects, adults could not supply food successfully to the young of artificially increased clutches. In species that lay more than one clutch in a season, clutch size may vary: for example, Pallid Swifts breeding in Tunisia average 2.89 eggs in the first clutch and 1.95 in the second. Studies of Edible-nest Swiftlets in Malaysia, however, revealed no significant differences between first, second and third clutches.

Swifts are naked when they hatch, most remaining so until their remiges and contour feathers erupt. However, while no swift species has natal down, the members of Cypseloidinae and Apodini show a fluffy nestling plumage of downy semi-plumes. In the case of the African Palm-swift, this adaptation is a result of the exposed nest-site, where the recorded temperature ranges from 15°C to 41°C. The Black and the Chestnut-collared Swifts both choose sites that are cooler and damper than the surrounding habitats, and their young are brooded continuously until the down appears, as with the three *Apus* species.

Weather affects the breeding biology of many swifts. Temperature, sunshine, wind velocity and precipitation all influence

In many areas the Chimney Swift does indeed nest in chimneys, as implied by its common name, but a range of natural sites is also used, including old woodpecker nesting holes. The nest itself is a very flimsy-looking half-cup made from short twigs, firmly cemented together and to the brickwork with adhesive saliva, and normally placed high up in some shady situation.

The normal brood consists of four or five young. Food pellets brought in to the nestlings have been shown to contain over 200 insects each, on average.

The chicks stay in the nest until they are about 30 days old, when they are ready to fly.

Towards the end of their nestling period, the young birds may creep out of the nest and hang tightly on to the nearby walls.

[*Chaetura pelagica*,
Indiana, USA.

Photo: R. Austing/FLPA]



feeding conditions and prey abundance. These factors change throughout the breeding season, affecting laying and hatching dates in the early stages, and nestling growth rates and, ultimately, the timing of fledging in the last phase. At a colony of Common Swifts in Nîmes, in south France, correlation of breeding success with 13 years of meteorological data suggested that rainfall and temperature were less important than north-north-west winds, which had a strong adverse effect on the abundance and ease of capture of prey, and hence on breeding success.

A similar study of Pallid Swifts in north-west Italy indicated that inclement May weather caused females to delay laying until June, although clutch size was not affected by either rain or temperature. The potential length of the breeding season plays a large part, as such a postponement is not an option for the Common Swift nesting farther north. In the latter, up to two days' delay in egg-laying has been noted, and this can be slightly longer if the clutch has not been started. Weather conditions do have some effect on the clutch size of the Common Swift, because in cold seasons two-egg clutches are more successful than those with three eggs. Furthermore, the Pallid Swift's fledging success declines during either very dry or very wet seasons, though the Mediterranean's more equable climate gives that species greater immunity to the weather than the more northerly Common Swift.

The nestling period of Common Swifts averages 42 days, though in poor summers it can extend to 56 days. If the weather is particularly bad towards the end of the breeding season, premature first flights can occur. Australian Swiftlets show the greatest weight gains after periods of rain. Nestling periods across the family are generally long in comparison with those of similar-sized birds, and do not show correlation with size. This long period in the nest is thought to be, in part, a function of the need for full independence after fledging. The longest known nestling period is that of the Spot-fronted Swift, which spends 65-70 days in the nest.

Brood-feeding varies quite considerably, even within a species. A swift brings back to the nest a bolus of insect food, which it then regurgitates directly into the throat of its young. This bolus

may be divided between chicks. It has been observed that, in the Apodidae as a whole, there are significantly more feeding visits per day the shorter the nestling period is.

Many variables affect brood-feeding rate, perhaps most notably the weather. Common Swift nestlings, and to a greater or lesser extent probably all those species breeding in areas where prey abundance varies, can survive long periods, even weeks, with little food. Their weight may drop by half under such conditions. Studies by D. M. Bryant and C. J. Hails showed that those species feeding at the greatest heights, and therefore on the most unpredictable supplies, stored the most fat while in the nest. In many species, a greater number of chicks in the nest stimulates an increase in feeding frequency, while in others the feeding rate varies with nestling age. In White-rumped and Chimney Swifts, feeding visits become more frequent prior to sunset, although the quantity of food decreases.

Experiments in which brood sizes of Common Swifts were manipulated to increase parental effort to different levels showed that, although greater brood size caused the adults to increase their feeding rate, food per chick decreased and both chick weight and parent weight fell. The parents with the largest broods dropped to a dangerously low weight, to which they responded by ceasing to feed their young. In all five nests where the brood was increased to four, and in two out of five where it was increased to three, brood reduction was observed. In these cases, the parents could not successfully raise their larger broods without risking their own survival; their decision to feed only themselves allowed them to survive and feed their remaining nestlings. Again, the tightrope between survival and mortality that results from the nature of the apodid diet is revealed. Although in this case the food-allocation problem resulted from experimental manipulation, swifts must cope with these problems regularly when faced with poor weather.

As previously noted, swift nestlings may be very fat. A high fat level helps them to survive lower feeding rates brought on by inclement weather. This situation, however, produces a physiological dichotomy. As A. Turner puts it, swifts must "juggle the demands of first being fat nestlings and then slim master flyers".

In the last week before fledging, nestlings lose weight to reach the perfect wing-loading and thereby effect a 10% increase in flight efficiency, with subsequent energy reductions and manoeuvrability enhancements.

The young of several species have been noted performing a variety of wing exercises before leaving the nest. In Böhm's Spinetail, which is recorded nesting in deep man-made pits, young birds have been seen clambering up the wall close to their nest, rapidly beating their wings, with frequent resting periods during which they supported themselves by using the tail. Another type of exercise is akin to human press-ups, with the body raised from the floor by outstretched and downward-inclined wings; at first, nestlings can hold this position only briefly, but as they grow they are able to prolong it, and it has been speculated that this may indicate readiness to leave the nest. Young African Palm-swifts are particularly precocious. They are restless within hours of hatching, and as early as the fourth day they climb away from the egg chamber onto the supporting flange, and from there up above the nest onto the palm frond.

Swift nests are kept clean by the combined efforts of parents and nestlings. Young White-rumped Swiftlets defecate over the rim of the nest from the first day of hatching, and the chicks of other species behave in a similar way, though not necessarily from such a young age. In the case of very young Chimney Swifts, the adults either remove the faeces from the nest or ingest them. Nests of Common Swifts become more soiled as the season progresses, as old faeces are not removed from the nest and eventually even fresh ones are ignored with greater regularity. Eggshells and dead eggs are typically ejected from the nest, although not apparently in the case of the three swiftlets in the study at Niah, in Sarawak. African Palm-swifts crush the shell into tiny pieces, which then fall from the nest.

Nest parasites are a feature of all swift species. Studies of White-rumped Swiftlets in Fiji revealed that louse fly (*Myophthiria fijiarum*) infestation was related to nesting density, chicks in the most isolated nests being free of the flies while the greatest fly numbers occurred where nests were touching. However, such ectoparasites may cause very little harm to their hosts. An ingenious experiment in England, at Oxford University, in which populations of the flightless louse fly (*Crataerina pallida*) and the

chewing louse (*Dennyus hirundis*) were artificially altered to produce a bimodal loading, showed that reproductive success and individual survival rates were independent of the level of ectoparasites. This is believed to be due to the fact that these parasites colonize new hosts by infecting offspring of adults (vertical transmission), so that any harmful impact upon the host will affect the survival of the parasite, too, by reducing the number of hosts available. However, particularly heavy infestations of biting lice can imperil swifts, especially if they are physiologically stressed, such as in the case of exhausted individuals on migration.

A number of predators will take both adult and nestling swifts. Young Atiu Swiftlets are sometimes killed by crabs, which even apparently knock the nests off the walls on some occasions. Various predators, ranging from African Red-winged Starlings (*Onychognathus morio*) to Spotted Eagle-owls (*Bubo africanus*), have been known to prey on the eggs or nestlings of the African Palm-swift.

Fledging success within the family varies from 26% in the latter species, with its comparatively vulnerable nest-site, to 96.1% in the Chimney Swift. Overall breeding success for African Palm-swifts is, however, only 17%, the same as for Black-nest Swiftlets, which produced only 0.2 young per breeding effort at Niah, a testament to the disruptive nature of nest-harvesting (see Relationship with Man). The effect of the weather upon nesting success of temperate-breeding species seems to vary, studies of Chimney Swifts suggesting that nestling survival relies less on suitable weather conditions than is the case with the Common Swift. It is interesting to speculate on what role helpers have to play in this reduced intimacy with climatic conditions, although the breeding success of the Chimney Swift does not seem to vary with the presence or otherwise of these helpers.

Swifts are long-lived birds with low mortality rates. The oldest ringed Alpine Swift was 26 years of age, while Common Swifts of 21 years and Chimney Swifts of 14 years have been recorded. As in many other families, mortality is much higher in the first year. On Gibraltar, a colony of Pallid Swifts showed a first-year mortality rate of 67.3%, compared with a subsequent annual rate of 26%. For Common, Chimney and Chestnut-collared Swifts, annual survival rates of, respectively, 81-85%, 83-85% and 71-81% have been recorded.



Alpine Swifts have adopted man-made nest sites to a much lesser extent than Common Swifts (*Apus apus*). Their natural nest-sites are mountain ledges, coastal cliffs and caves, but they do regularly nest on buildings in southern European towns and cities, as here in Italy on a wooden beam in the roof of a school building. Indeed, some cities, notably Istanbul, have very large urban populations of Alpine Swifts. Like most of the members of Apodidae, the Alpine Swift is a long-lived species, the oldest recorded bird having reached an age of 26 years.

[*Tachymarptis melba melba*, Varese, Italy.
Photo: Claudio Galasso]

When threatened on the nest, a young swift will often raise its wings in an aggressive display, as demonstrated by this Black Swift. Young swifts are raised on a very rich diet of insects, which promote rapid growth. The frequency of feeding depends very much on the success of foraging, and thus on the weather.

The nestlings of some species are, if necessary, able to survive for weeks with very little food, largely due to their tendency to lay down layers of fat during periods when food is plentiful: during spells of bad weather the birds draw on these reserves in order to maintain their rhythms of growth. One direct consequence of this strategy is that in normal conditions the chicks grow decidedly fat, which in time would clearly be a distinct disadvantage for the day when they launch themselves into mid-air and embark on a highly aerial way of life. In order to meet this problem, over the last week or so of the nestling period they start to lose weight. During this same period, the birds perform a series of wing exercises in order to bring themselves into trim. One of the most remarkable of these involves a form of press-up, in which the bird stretches out its wings and tries to lift its body off the ground!

[*Cypseloides niger borealis*,

San Jacinto Mts,
California, USA.

Photo: Manuel Marín]



Movements

The extreme seasonal variability of insect abundance in the temperate zone forces long-distance migration on the majority of those species breeding outside the tropics. Within the tropics, post-breeding dispersal and altitudinal and pursuing movements are commonplace, while diurnal foraging movements on a variety of scales are a feature of this family. All species usually migrate in flocks, which may be small or large. Migration can be very rapid: one Common Swift is known to have migrated 1275 km in four days, while the larger and even faster Alpine Swift was proved on one occasion to have moved 1620 km in three days.

Some migration occurs at night. At Fraser's Hill, in Malaysia, several migrant species of swift have been captured after being attracted to bright security floodlights. Migration occurs on a broad front, with little funnelling at narrow sea-crossings. Indeed, it is believed that Black Swifts that have bred in North America may migrate from Central America into South America over the eastern Pacific, basically cutting the corner, and Chimney Swifts leaving eastern North America pass regularly over the Caribbean, earning their specific name *pelagica*. Migration often takes place at high altitude, and becomes apparent only when poor weather forces flocks down.

Long-distance movements by temperate-breeding species are not confined to annual migrations. Swifts will undertake major



An unusual sight in modern times is to see Common Swifts using a "natural" nest-site, for instance, as here, a hollow in a broken tree. The extraordinary success of this species in adapting its nesting habits in order to make use of man's buildings has led to its nesting almost exclusively in man-made sites nowadays. In some areas, humans have even taken more active steps to help the local swift populations by setting up specially designed nestboxes; these tend to be rather narrow and also prove attractive to bats.

[*Apus apus apus*, Sweden.
Photo: Uno Berggren/
Ardea]

movements to escape adverse weather at any time of the year, and these occur on a number of scales. For instance, Common Swifts fly ahead of storm fronts before they cross them, returning to their breeding grounds in the relatively clement weather behind the front. It has also been noted that swifts take advantage of the relative abundance of aerial plankton in these situations, caused by updraught associated with convection. Escaping from low-pressure systems can take much longer, not least because swifts can react to an oncoming cold front that is still 500 km away. These movements are presumed to be triggered by various meteorological factors which in turn bring about a reduction in food supply. The birds fly into the wind, hence in the Northern Hemisphere circling in a clockwise fashion, usually into the warmer areas south or south-west of the depression. One of the most celebrated examples of such food-driven nomadism comes, again, from the Common Swift, whose mass movements around depressions in the breeding season to avoid rain can entail round trips of up to 2000 km. Tens of thousands of Common Swifts can be involved in a single group, leaving the breeding grounds for days or even weeks, and birds from southern England have been known to feed as far afield as Germany at such times; many of these individuals will be non-breeders, but parents are often involved, utilizing their fledglings' ability to survive long periods without food (see Breeding). Black Swifts in North America are known to undertake similar flights, which may be common throughout the family, particularly among those species that occur in temperate climates.

Various strictly tropical species also undertake annual migrations, as well as more nomadic wanderings. The White-collared Swift and some African species have been noted making pursuing movements, taking advantage of the abundance of insects disturbed by savanna fires during the dry season. For Common Swifts, at least, arrival on the sub-Saharan wintering grounds does not signal the end of their travels: complex intra-African migrations, often involving escape movements, take place throughout the winter.

Diurnal movements to suitable foraging habitat are typically much shorter, and often involve a daily flight from a roosting or nesting site lacking adequate food supplies, or perhaps to a particular site with an abundance of food. This phenomenon is readily seen in the area around the Rift Valley lake of Naivasha, in

Kenya. During the day, huge numbers of Nyanza Swifts (*Apus niansae*) and lesser numbers of Mottled Swifts feed over the lake, where there is an abundance of insect prey; in the evening, they return in their tens of thousands to the nearby, though relatively arid, savanna-filled Hell's Gate Gorge to roost. Similarly, many swiftlets breeding on offshore islets undertake daily journeys over the seas to suitable feeding habitat.

As with so many aspects of behaviour in this family, the timing of migration can be greatly affected by the impact of climatic vagaries upon the aerial plankton which forms the diet of all swift species. The most striking example came from Finland in the autumn of 1986. Most of the Common Swifts had left as usual by late August, but as many as 2000 adults apparently "returned" in mid-September; they commenced the moult that they usually undergo on their wintering grounds and eventually died, either from starvation or as a result of the November frosts. It is thought that the unusually bad weather in the autumn of that year prevented the birds from accumulating sufficient fat deposits for them to undertake their long southward migration. Another case of mass mortality was recorded on the small and remote Islas del Cisne (Swan Islands) in the Caribbean, 180 km off Honduras, when a flock of some 200-300 Chimney Swifts died over the course of a week in October. The low level of insect life on the islands was indicated by the emaciated state of the birds collected.

The extreme mobility of swifts has assisted their colonization of the globe. Even many of the comparatively sedentary swiftlets inhabit oceanic islands that have never formed part of any continental landmass, while the family enjoys a near-cosmopolitan distribution. It is fair to state that, with the exception of some island groups, every site that can support some species of swift does so. The near-ubiquity of the Apodidae stands testament to avian dispersive power. Vagrancy is the most obvious manifestation of this attribute, and it is perhaps our only means of observing fluctuating distributions, and changing migratory pathways, in the geological instant that is our lifetime.

Sometimes, these episodes of vagrancy will lead to colonization, perhaps even rapid colonization, of a new area, if conditions are right, as can be seen in the case of the White-rumped Swift in Spain, the Pallid Swift in southern Europe, and the African Palm-swift in southern Africa. On other occasions, the arrival of an individual thousands of kilometres away from its typical

areas of occurrence will tempt observers to form elaborate theories that fit only a regional view of the issue.

In short, the poorly termed phenomenon of vagrancy is nothing more than individual variation in migratory behaviour, writ large. It acts, unconsciously, as a mechanism that allows for range expansion. The global environment is not renowned for periods of equilibrium, and on a superficial level one might say that any species attempting to hold back the inevitability of extinction will respond to this environmental change, or that a species that sits still will hasten its own demise. The work of P. Berthold and others has proved the high heritability of migratory-goal direction, and this may help to explain patterns of vagrancy. Those individuals that take the opportunity to sample life away from the strongholds of their species are very likely to produce no offspring, but they may presumably gain temporarily from a lack of competition for resources. If they survive long enough to breed, the chances of their offspring undertaking a similar journey will be higher than if these had had different parents.

The history of, for example, the Plain Swift, which breeds primarily in the Canaries and Madeira, would seem to be similar to that which has been proposed for the Hawaiian Goose (*Branta sandvicensis*). Common Swifts and their recent ancestors must have strayed to the Canaries on countless occasions throughout the Quaternary, as they do regularly to this day. The evolution of the Plain Swift is proof that some did, indeed, stay long enough to breed in the hospitable climate of those islands. Subsequent natural selection in isolation, no doubt exacerbated by the founder effect, accounts for the morphological differences between the two species. Interestingly, Common Swifts are now believed to be nesting on Gran Canaria, where a few have been present during the breeding season in recent years.

Spectacular cases of vagrancy have been recorded for a number of species. Trans-Atlantic vagrancy is well established among swifts and, unlike in most other landbirds, has involved westward as well as eastward movements. Alpine Swifts have been recorded in the Caribbean on at least three occasions, while there have been several Chimney Swifts in Europe, as well as records from Greenland and Tenerife. White-throated Needletails have been found in Europe on more than a dozen occasions, as well as in the Aleutians and the Seychelles. The latter archipelago has in fact been visited by several continental swift species. Common Swifts have reached

the Pribilof Islands, off Alaska, and many oceanic archipelagos, including the sub-Antarctic Prince Edward Islands. Pacific Swifts (*Apus pacificus*) from eastern Asia have occurred at least ten times in Alaska and, more remarkably, twice in Britain. The western North American Vaux's Swift has strayed on a number of occasions to the eastern seaboard, the Ashy-tailed Swift (*Chaetura andrei*) has been recorded on the remote Falkland Islands, and a Black Swift, probably of Caribbean origin, strayed as far north in the USA as Martha's Vineyard, in Massachusetts. Other notable incidents of overshooting have been recorded for the southern Mediterranean White-rumped Swift, which has occurred in Scandinavia, while Alpine Swifts are annual vagrants to the British Isles. Seemingly sedentary, island-bound species are also capable of the odd surprise, Antillean Palm-swifts having been found in the Florida Keys and on Puerto Rico.

Relationship with Man

Few families have such an ambiguous relationship with man as the Apodidae. On the negative side, human destruction of habitat has greatly diminished foraging areas for some species, while over-harvesting in the lucrative bird-nest trade is taking its toll on South-east Asian swiftlet populations, and insecticides and herbicides have severely reduced both the range and the number of insect prey in many areas. At the same time, many species have found ready-made nest-sites in buildings or benefited from the spread of palm trees, essential as nesting sites for some swifts.

Many species have taken advantage of artificial sites, and some no longer use traditional sites to any extent. For example, in a report of a Chimney Swift nesting in a hollow silver maple (*Acer saccharinum*), the observers noted that fewer than ten incidents of tree-nesting had been recorded in the previous 100 years. The use of buildings has not only improved nesting success, perhaps as a result of nest-site security, but has also facilitated range expansions in several species.

The extent of this evolutionary opportunism and the near-total conversion of many species to artificial nest-sites are leading to problems closely akin to those experienced by many bat species. In the case of the Common Swift, roofing repairs are seldom undertaken with the welfare of the birds in mind. Ex-

The Alpine Swift is one of the great migrants among the Apodidae, its breeding grounds stretching north into southern Europe and up to Central Asia, with most birds wintering in tropical Africa. It tends to migrate at high altitude, and it is frequently the case that its movements are observed only when wet weather or wind forces the birds down. Even on a local scale, its mobility is notable, and birds regularly cover long distances, estimated at perhaps 1000 km each day. One migrating Alpine Swift was recorded as covering 1640 km in a matter of only three days.

[*Tachymarptis melba melba*,
Punta del Hidalgo,
Tenerife, Canary Islands.
Photo: R. F. Porter/Ardea]



tending roofing felt, inserting concrete fillets under tiles, and putting anti-insect meshing into air-bricks may benefit the human inhabitants, but such actions have contributed in many parts of Europe to a decline in swift populations.

A British Trust for Ornithology initiative, "Concern for Swifts", has highlighted the dilemma, and as a result some local council authorities have introduced "swift-friendly" measures such as incorporating swift boxes into eaves. In some places, such as Amsterdam, in the Netherlands, it has long been an offence to obstruct the nest entrances of swifts. However, such measures, though welcome indeed, are unlikely to reverse the downward trend unless legislation, preferably at a supranational level, is introduced.

It is doubtful that any wild birds are so financially important as the swiftlet species that produce the so-called edible nests. These nests, composed primarily or, in the case of the aptly named Edible-nest Swiftlet, entirely of saliva, have long been considered a delicacy in Chinese cuisine and form the main ingredient of the famous bird's-nest soup. This trade in nests dates back at least to the late Ming and early Ching dynasties of seventeenth-century China. Some claim a far longer history and believe that these nests may have been consumed in China as long ago as AD 500, while there is some evidence that trade with Sarawak may go back to the year AD 700. It is apparent, however, that in recent decades the populations of these birds have not managed to match the insatiable demands of this multi-million-dollar industry.

Over-harvesting and destructive harvesting have long been problems. Estimates from Gomantong Caves, in Sabah, during the 1959 collecting season suggested that 190,000 eggs and nestlings were destroyed as harvesters simply threw them from the nest to the cave floor. Insensitive practices have caused a decline in the famous Niah Cave colonies of Sarawak, which at one time were thought to number 4,500,000 birds; estimates from the late 1980's and early 1990's put the Niah population of Black-nest Swiftlets at somewhere between 150,000 and 298,000 birds. As might be expected, falling swiftlet populations have reduced the annual nest harvests. Yet there is little wonder that the trade is perpetuated, as the export value of this commodity to the Sarawak economy was US\$10,400,000 in 1995, with some owners of the customary rights for Niah earning up to US\$20,000 per annum solely from this source. The main producer, Indonesia, is thought to export nests worth as much as US\$1,060,000,000 per annum.

On a global scale, in 1989, a total of 19,900,000 swiftlet nests was traded across state boundaries, and that in addition to those nests used in the countries of origin. The vast majority of this trade is centred upon Hong Kong. A staggering 18,700,000 and 17,500,000 nests were imported into Hong Kong in 1990 and 1991, respectively, with a relatively small proportion being sold to other countries; indeed, in 1989, as many as 25,000,000 nests were consumed in Hong Kong alone. The cost of these nests is truly astronomical. In the early 1990's, good-quality nests could fetch over US\$1225 per kilogram, although figures of US\$367-611 were more typical. During the 1980's, between 81,000 and 160,000 kg of nests imported into Hong Kong had a value of between US\$5,000,000 and US\$39,000,000. Astonishingly, it is now thought that prices could be as high as US\$36,000 per kilogram. To put this into perspective, between 80 and 120 nests make up 1 kg and it is thought that Indonesia alone may harvest 200 tonnes annually, which would represent at least 16,000,000 nests. Not surprisingly, such exploitation of nests has had a severe impact on the populations of a number of swiftlet species (see Status and Conservation).

With such huge figures involved, it is equally predictable that "dirty business" surrounds some of the operations. In 1998, the *Bangkok Post* denounced the enormous sums being made by the concessionaires and also the Thai government department that issues the concessions, while no benefits whatsoever passed to the local human populations. Indeed, the locals are actually banned even from landing on such islands, a prohibition which, it is claimed, is sometimes enforced even by means of "legalized murders" that are subsequently passed off as self-defence. As if this were not enough, in 1996 the largest concessionaire declared exports of 700 kg, whereas the records



The Brown-backed Needletail breeds in the Indian Subcontinent, Sri Lanka and the Greater Sundas. It is a partial migrant, some of its populations or individuals making regular movements, while others essentially stay put all year round. It is a very large swift with a bulky body, a protruding head and prominent tail spines; the characteristic white undertail-coverts and flanks are clearly visible in flight.

[*Hirundapus giganteus indicus*,
Khao Yai National Park,
Thailand.
Photo: Morten Strange]

of the Customs Department showed that the overall figure for this company, together with its smaller competitors, was way up at 9000 kg! Collectors apparently harvest the nests twice during the season, so that the swiftlets are forced to build three nests if they are to have any hope of breeding, while another consequence is that their salivary glands are so exhausted that the third nest is often stuck together with blood and other materials too. Despite legal protection and purported control of the trade, it seems difficult to imagine that the swiftlets can sustain such an onslaught indefinitely.

The swiftlets' much-sought saliva may turn out to have other uses for humans too. It has recently been suggested that one particular water-soluble glycoprotein found in this saliva may prove to be a useful adjunct to existing drugs used in combating immunodeficiency in AIDS, as it is thought to promote cell division in the immune system.

Finally, turning to quite a different matter, it is hard to estimate the beneficial effects of swifts, or indeed of any insectivorous species. Their readiness to take advantage of short-term concentrations of food indicates their special potential as natural pest-controllers. Large numbers of Little Swifts and Asian Palm-swifts have been observed feeding on certain insect pest species during infestations in southern India, but dusting of the areas over which these swifts were voraciously feeding with a cocktail of pesticides caused a massive reduction in the frequency of foraging. Studies of House Swifts in Yunnan showed that 67.5% of all insects eaten by this species were agricultural pests, while only 13% were beneficial, and studies of Pacific Swifts in China have yielded similar results.

Status and Conservation

Six species of swift are currently considered threatened, but differing taxonomic views swell this figure to eight, while another three taxa are listed as Near-threatened and three more as Data-deficient. Although as many as five of these 14 swift taxa are not given full specific recognition by all authorities, this should not in any way reduce the importance of the case for the conservation of each. Management programmes for their protection are typically hindered by lack of detailed biological data.

Of the six species classified as Vulnerable, the White-chested Swift (*Cypseloides lemosi*) was described as recently as 1962, when it was observed in the field and collected in the Upper Cauca Valley of south-west Colombia. Recent sightings in north-central Colombia, as well as farther south in north-east Ecuador and north-west Peru, suggest, however, that its distribution may prove to be more extensive than was previously thought. The species' ecological requirements are unknown, although it has been noted foraging over eroded grassy hills with scattered scrub. This habi-

tat is believed to be increasing in area, perhaps as a result of deforestation in the region.

The Seychelles Swiftlet (*Aerodramus elaphrus*) is threatened not only by the lack of sites, but also by an unfortunate cocktail of problems: predation by introduced species, especially cats, and Common Barn-owls (*Tyto alba*), as well as human disturbance, both accidental and deliberate. Although only six colonies are known, it is considered likely that undiscovered colonies exist and the total population, based on 1996 and 1997 figures, is thought to number roughly 2500-3000 birds, with about 2263 individuals on Mahé (including some 500-600 at La Gogue), about 79 pairs on Praslin and 35-45 pairs on La Digue. A recent increase on the last of these may be the result of changed hydrological conditions or of immigration from Felicite, where a colony has disappeared.

Confined to the Philippines, Whitehead's Swiftlet (*Aerodramus whiteheadi*) is a Vulnerable species whose true rarity was clouded for many years owing to the misallocation of other taxa within this species. It is known only from Mount Data, on Luzon, where four specimens were taken in 1899, and Mount Apo, on Mindanao, where three specimens were collected in 1904. After an absence of some 90 years, a series was recently collected from South Cotabato, on the latter island. This species is believed to be threatened by habitat loss.

The Atiu Swiftlet, which may yet prove to be a race of the White-rumped Swiftlet, was discovered in 1973, when the single known cave, on Atiu Island in the Cook Archipelago, contained 60 nests. A census in 1987/88 revealed a total of 190 nests in two caves. Although the swiftlet's numbers are believed to be stable, disturbance by tourists, even on such a remote island, may present a problem.

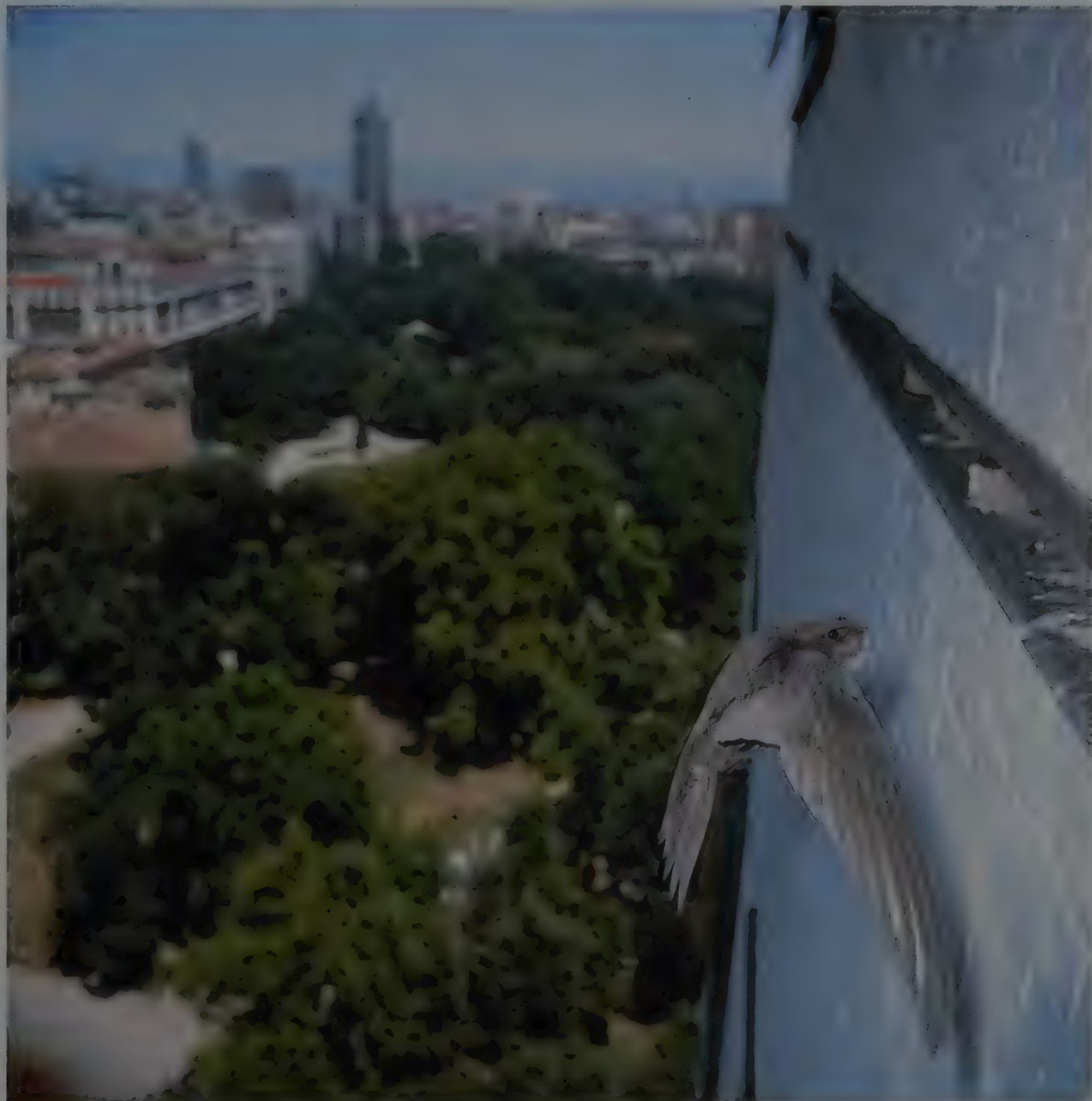
Schouteden's Swift (*Schoutedenapus schoutedeni*), known from only five specimens, is one of several rare species inhabiting the Itombwe Forest area of eastern Zaire, and it too is listed as Vulnerable. It has not been recorded since 1959, and the difficulties of field identification suggest that further information would need to be gleaned by trapping. As so little is known of its sole congener, the comparatively abundant, though confusingly named, Scarce Swift, it seems likely that, if Schouteden's Swift does still exist, it may be many years before it surrenders its secrets.

The Dark-rumped Swift (*Apus acuticauda*), also listed as Vulnerable, was first collected in Nepal, although there is some speculation that the specimen may actually have come from India. It is known with certainty to breed only in the Khasi Hills of Meghalaya, north-east India. In the past, at least, it appears also to have bred in Assam, on the strength of a series of specimens collected in the Lushai Hills; these birds were apparently breeding at a different time of year from those in the Khasi Hills, on

A Common Swift returns to its nest on the 16th floor of a modern building in Milan. In this case the swifts are making use of the narrow air-conditioning vents set into the brickwork. These offer a safe, inaccessible site for their nests, and in many respects might be considered structurally similar to part of a natural cliff. From here the birds make regular flights in the surrounding airspace, searching for flying insects; this bird is returning with its crop full of food for the young.

[*Apus apus apus*, Milan, Italy.

Photo: Paolo Fioratti/Oxford Scientific Films]



the basis of the different timing of moult. The species was recently recorded in Bhutan, in the springs of 1996 and 1997, and it is still occasionally reported from Thailand in the winter. The lack of biological study of this species, however, gives little indication as to how stable this small population may be.

Another South American *Cypseloides* species, the indistinct Rothschild's Swift (*Cypseloides rothschildi*) of north-western Argentina and perhaps elsewhere, is listed as Near-threatened, although very little is known of any aspect of its ecology or current status, and even its distribution remains most inconclusively defined. This is due in no small part to the great difficulty of identifying it in the field.

The Waterfall Swift is another Near-threatened species. It is restricted to the Sundaic region, where it is known from a small number of sites. Its stronghold is the Cibereum Waterfall in the Gunung-Gede/Pangrango National Park, in western Java, where 60-80 birds were recorded in August 1985; the species is also regularly seen at the Letter W waterfall near Gunung Kerinci, in Sumatra, with up to eight seen in 1991. It may prove to be more widespread in Sumatra: as well as more historical records, a group of eight was recorded at Gunung Leuser in the north in July 1986, with seven during October, and two were seen at Brestagi in February 1994. In addition to historical Bornean specimens, this species has been recorded in recent years from the Mount Kinabalu National Park, in Sabah.

Like the Seychelles Swiftlet, the other island swiftlet of the Indian Ocean, the Mascarene Swiftlet (*Aerodramus francicus*), is also rare, but it is currently classified as Near-threatened. While seemingly restricted by a lack of suitable breeding sites, it is actually relatively abundant within its small range, although a number of colonies on Reunion are threatened by the activities of speleologists.

One of the most contentious taxonomic cases is that of the White-fronted Swift (*Cypseloides storeri*), currently listed as Data-deficient, from the sierras of south-west Mexico. Since its description as a new species in 1992, based on a bird collected from the tent of the describing scientists, and the subsequent discovery of further specimens in museums and a mummified individual collected from a dried stream bed, there has been much debate as to this form's relationships and even its migratory status. One of the major players in this debate has recently documented a probable field sighting of this swift. Even if it does prove to be a race of the White-chinned Swift, or merely just a geographically isolated population, its apparent rarity in this region still justifies further study.

The Data-deficient Mayr's Swiftlet (*Aerodramus orientalis*) is another enigmatic species, known from only three specimens. These were collected from such widely separated island locations as New Ireland in the Bismarck Archipelago in 1935, Bougainville in the western Solomon Islands in 1979, and Guadalcanal in the eastern Solomons in 1962. The lack of any additional data makes it difficult to know whether this geographical pattern indicates a mere relict of a much wider range or whether the species might be found on intervening islands. Interestingly, in July 1987, a large unidentified swiftlet was recorded on New Georgia in the central Solomons, and small numbers of a large swiftlet thought to be Mayr's were recorded in mid-May 1989 on Manus, in the Admiralty Islands (western Bismarck Archipelago).

Of the forms listed as threatened but not herein considered full species, the race *vulcanorum* of the widespread Himalayan Swiftlet (*Aerodramus brevirostris*), commonly known as the Volcano Swiftlet, is considered Vulnerable. Historically it was confined to volcanic peaks in Java, but all recent records are from a single locality, Gunung Gede. The restricted nature of its habitat requirements and its limited distribution imply that it has never been truly common. Its predilection for nesting within the craters of active volcanoes ensures that periodic extinction is the fate of many colonies.

The Tahiti Swiftlet, the nominate race of the Polynesian Swiftlet (*Aerodramus leucophaeus*), is restricted to Moorea, where it may be only a vagrant, and Tahiti. It too is classed as a Vulnerable form, one which formerly occurred also on Huahine Island, and which has declined throughout the twentieth century. It is believed that the loss of both chicks and eggs to the introduced Common Myna (*Acridotheres tristis*) may be a sig-

nificant contributory factor in this decline. In 1984, an estimate of only 200-500 individuals was made, and a survey between 1986 and 1991 located this swiftlet in only six out of 39 suitable valleys on Tahiti.

The Bioko Swift, the race *sladeniae* of the African Swift (*Apus barbatus*), is classed as Data-deficient and, like some of the preceding species, is known from only a handful of specimens. It has been collected from a wide area: the Obudu Plateau in south-east Nigeria, Mount Kupé in western Cameroon, the island of Bioko (Fernando Póo), and Mount Moco in Angola. Six of the ten specimens are from Bioko, where they were collected in December 1903 and early January 1904, and it has been suggested that this form may be only a vagrant to the island from which it was named, rather than a resident. It may also occur in Liberia. The scarcity of field sightings, coupled with the taxonomic uncertainty of this swift, justifies its categorization.

Other, less threatened species are afforded protection by various national laws, and in some cases by international treaties. Within Europe, the Plain Swift is designated a Species of European Conservation Concern, Category 4, since over 50% of its population is found within the European Community. The Pallid and Alpine Swifts are given Provisional threat status. The Guam Swiftlet (*Aerodramus bartschi*) is protected by the US Federal Endangered Species list 1984. The recent decline in the Sri Lankan population of the Indian Swiftlet, despite strong laws with severe, though welcome, consequences (see below), is a salutary reminder that legislation alone will not be enough to protect any species, let alone the rarer ones.

The collecting of and trade in nests of swiftlets (see Relationship with Man) has led to serious concerns for the future of some species, at least locally. In response to the dwindling populations at Niah, a complete ban on harvesting was imposed between 1989 and 1991, with a further four-year extension from 1993. Despite this, the downturn in numbers continued, due in no small part to considerable poaching. It goes without saying that, if such high-profile sites cannot be adequately protected, then smaller sites, with no monitoring, must suffer enormously. Indeed, along the Andaman coast of Thailand, poaching is rife on the myriad small limestone islands honeycombed with suitable caves for nest-sites. Many of the islands are leased to collectors, and in the early 1990's one businessman paid US\$1,500,000 for the rights to collect on approximately 60 islands. The conflict between the authorized collectors and the poachers may have considerable human cost, too, with many reports of shoot-outs between the adversaries, not to mention the danger of climbing to the roof of massive caverns, supported only by bamboo structures.

A decline in the population of Edible-nest Swiftlets has occurred on the Nicobars since the Indian government began settling people on these islands in the late 1960's. Traditional "swiftlet-friendly" harvesting practices have been replaced, and further problems have been caused by the activities of poachers from Thailand. In addition, those caves that have witnessed declines in this species have seen increases in Glossy Swiftlets and a bat species. R. Sankaran believes that inclusion in Appendix I or at least Appendix II of the Convention on the International Trade in Endangered Species (CITES) would be helpful, but notes that "protection alone may not help populations to recover because an increase in numbers will be possible only if the Edible-nest Swiftlets outcompete the other two and regain nesting space".

National protection in Sri Lanka, where Indian Swiftlets have been protected by law since 1963, with an amendment made in 1993 increasing the penalties for disturbance, has not stemmed the illegal trade that resumed as recently as 1993, despite a record fine of US\$370,000 in 1995. This fine resulted from the seizure of nests weighing 44 kg, bound for the Far East.

None of the swiftlet species producing edible nests has protection under international law. In November 1994, at the Ninth Conference of Parties signed up to CITES, Italy proposed that all of these species should be placed on Appendix II, but this was later withdrawn. Despite the gloomy scenario so far depicted, it seems that there may, ultimately, be some hope. So-called swift houses, purpose-built structures for swiftlets to nest in, have been developed in Indonesia and used with great effect. The struc-

The Seychelles Swiftlet is restricted to the islands of Mahé, La Digue and Praslin in its namesake island group, where it nests in caves. The total population is believed to be of the order of 2500-3000 birds, and like some other rare Seychelles birds it is threatened by the introduction by alien predators, notably cats and Common Barn-owls (*Tyto alba*). The Seychelles Swiftlet forages widely over the forests and wetlands in search of insects.

[*Aerodramus elaphrus*,
La Digue Island,
Seychelles.
Photo: David Hosking/
FLPA]



tures are first occupied by Glossy Swiftlets, which act as surrogate parents to the eggs of Edible-nest Swiftlets which are placed inside. The hatchlings of the latter species return as adults to the artificial structures and establish colonies.

Beyond the bird's-nest trade, swifts are not otherwise commonly the target of deliberate human interference unless they occur in densities that allow for easy capture. There is a record of a swift being killed with a bow and arrow in Zaire, and in Thailand swiftlets have been picked out as targets by catapult-users. Such opportunistic human predation probably has little impact upon swift populations. In the Philippines, however, large numbers of Purple Needletails are apparently killed on occasions when feeding around bee hives, and Common Swifts in Malawi are netted and eaten. Similarly, the huge flocks of Scarce Swifts that sometimes feed low over the ground are exploited as a food source by people using nets, and are even killed by being struck with sticks. In some Liberian villages, thatched constructions 3-5 m high are provided for the use of African Palm-swifts, at least in part to enable the villagers to take and eat the young. In Spain, a technique for catching swifts for food involved flying a kite trailing a hook baited with grass, which the swifts took for nesting material, facilitating their capture.

Accidental death resulting from human activities is more frequent. Swifts sometimes collide with man-made obstructions such as telephone wires. There is also an example of a Great Dusky Swift (*Cypseloides senex*) hitting a plane, a hazard which has also proved fatal for aerial-roosting Common Swifts. A worrying case from Africa concerns African Palm-swifts dying after drinking chlorinated water from a swimming pool. How many other birds die in this way? Species that nest and roost in chimney sites often suffer from burning and asphyxiation. Members of a small colony of Short-tailed Swifts breeding in one Bolivian chimney fell into the fireplace on a number of occasions.

More disturbingly, there is some evidence that swifts are the recipients of dangerous levels of pesticides, in much the same way as are various raptors. On the Pacific island of Guam, the endemic Guam Swiftlet has been recorded with body-tissue concentrations of DDE averaging 0.27 ppm. The notorious pesticide DDT is soluble in body fat and forms the highly stable compound DDE. This pesticide is one of several that have been proved to reduce breeding success in a number of birds of prey. When one considers the relative position of swifts in the food chain, and their longevity, it stands to reason that pesticides pose a risk to this family.

Several forest species show signs of contracting ranges. In some instances, they can no doubt feed with similar success over second-growth as opposed to primary forest, but the removal of mature trees with suitable niches for nesting has presumably affected many forest species. The importance of such mature trees is illustrated by the case of African Swifts, which will continue to use large trees for nesting and roosting despite the clearance of other trees around them. It has even been postulated that the complete removal of old growth from forest in parts of western North America may lead to the regional extirpation of Vaux's Swift.

Most controversial is the effect of potential human-induced climate change on swift populations. The role of temperature and precipitation in providing suitable breeding conditions, primarily an adequate arthropod food supply, is undeniable. If current models of climate change are to be believed, a global change in climate would undoubtedly have a profound effect upon these birds. Observers looking for evidence of global warming could point to the spread of such traditionally tropical species as the House Swift, the Little Swift and the White-rumped Swift into relatively northern, and indeed also southerly, climes. Such biogeographical evidence, however, suffers from the same deficiencies as the meteorological evidence. Our database covers but a brief instant of geological time. Intuitively, we believe that human activities must affect the climate and the patterns of avian distribution, but have the ranges and populations of swifts, seemingly climatic litmus papers, waxed and waned throughout the Quaternary?

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Subfamily CYPSELOIDINAE

Genus *CYPSELOIDES* Streubel, 1848

1. Chestnut-collared Swift

Cypseloides rutilus

French: Martinet à collier roux German: Rothalssegler Spanish: Vencejo Cuellirrojo

Taxonomy. *Hirundo rutila* Vieillot, 1817, Guyana.

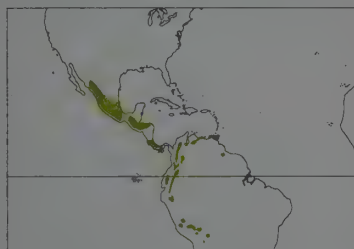
Forms superspecies with *C. phelpsi*. It has recently been suggested that present species, probably along with less studied *C. phelpsi*, be included in *Streptoprocne* due to similarities in clutch size, development of young, and plumage, and these details would certainly suggest a close link with that genus: species formerly placed in *Chaetura*. Race *brunnitorques* rather similar to nominate, and may be synonymous. "*Chaetura nubicola*" is synonym of present species. Three subspecies currently recognized.

Subspecies and Distribution.

C. r. griseifrons (Nelson, 1900) - W Mexico.

C. r. brunnitorques (Lafresnaye, 1844) - SE Mexico to Bolivia.

C. r. rutilus (Vieillot, 1817) - Venezuela to Guyana and Trinidad.



Descriptive notes. 13 cm; 21 g. A medium-sized swift with a broad, shallowly forked tail and rather broad wings; blackish plumage, slightly paler below; most apparent features are dull red throat and collar; some brown feathers admixed on ear-coverts and on centre of throat. Female has shallower tail-fork on average than male, with collar partial or lacking; birds lacking collars tend to have generally paler plumage. Juvenile very similar to collarless form of female in both plumage and structure. Race *brunnitorques* probably averages longer-winged; *griseifrons* is paler than *brunnitorques*, with sootier upperparts and

underparts as well as pale-fringed forehead, superciliary area and lores.

Habitat. Mainly montane, occurring up to 3400 m in Andes. Typical altitudinal range: Ecuador, W slope 500-3000 m (nesting up to 2300 m), E slope 500-2000 m; Mexico 1500-3000 m; will feed over lowlands, especially when rain falling in highlands, on occasions right down to sea-level. Main habitats defined as montane evergreen forest, secondary forest and second-growth scrub. Feeds over both forested and cleared areas, frequenting ravines and more gentle landscapes.

Food and Feeding. Specimens collected N Venezuela contained numerous *Crematogaster* ants. Highly gregarious. Often flocks with other swifts, especially *Streptoprocne zonaris* with which forms large pre-roosting flocks. Tends to forage in upper strata of mixed swift flocks, at least in Ecuador. In S Colombia (Cauca), recently seen feeding in mixed flocks with *S. zonaris*, *C. niger borealis*, *C. lemosi*, *C. cryptus* and *C. cherriei* on immense swarms of various small beetles during late Sept to early Oct.

Breeding. In Trinidad mainly May-Aug; in Colombia collected in breeding condition early Jun; in Costa Rica egg-laying mid-May to early Jul, not starting with first rains but delayed until heavier rains May/June; in Trinidad if another nesting attempt made during season, interval between ending of previous attempt and laying first egg of new clutch 0-25 days, majority 6-15. Closely associated with water, 50-300 cm above which it nests in shaded sites with humidity never falling below 95%; sea caves used in Trinidad; strong nest-site fidelity. Nest form varies with substrate, typically half-cupped with shallow central depression; consists almost entirely of mosses and liverworts with mud used at base or point of attachment; dry mosses and liverworts used as nest lining and may be added while nest in use; sited on tiny ledge, rock protrusion or niche on rock-face which can be overhanging or vertical. Mean nest measurements, Costa Rica: height 126 mm, width 104 mm, front to back 98.5 mm, central depression 31 x 66 mm. Two eggs; incubation 24-26 days; interval between deliveries of food to chicks typically at least 100 minutes; fledging 40-42 days. Average breeding success 36-40% with 0.9-1.3 young fledged per breeding effort.

Movements. Partial migrant. Resident South and Central America from Honduras N. Situation in Honduras, at least, may be equivocal as not known if wintering population there has bred farther N. Central American populations not reported in South America. Limited withdrawal in winter from N Mexico, especially high-altitude interior during Oct-Feb, at least, with apparent migrant flocks observed W Mexico, mid-Mar to May. Specimens from Guatemala taken from mid-Jul to Oct.

Status and Conservation. Not globally threatened. In general, considered to be a rather local species, apparently more abundant within its South American range, where it can regularly be encountered, often in larger numbers, than within its Central American distribution. However, species is locally common in Costa Rica and it appears to have been recorded more often in recent years from Panama. Recent research in Ecuador shows it to be at its greatest densities on the west temperate slope. Occurs in several protected areas throughout its extensive range, e.g. Monteverde Biological Reserve (Costa Rica), La Planada and Rio Nambi Reserves (Colombia), Podocarpus National Park (Ecuador) and Asa Wright Nature Centre (Trinidad); also regularly recorded at Macchu Picchu (Peru).

Bibliography. Beebe (1947, 1949), Belcher & Smoother (1936), Best & Clarke (1991), Best *et al.* (1993), Binford (1989), Bloch *et al.* (1991), Collins (1963, 1967a, 1967b, 1972a, 1974, 1980b), Fjeldså & Krabbe (1990), Gilliard (1941), Herklots (1961), Hilty & Brown (1986), Howell & Webb (1994, 1995a), Howell *et al.* (1997), Kiff *et al.* (1989), Krabbe & Somoza (1994), Marín (1993), Marín & Stiles (1992), Meyer de Schauensee & Phelps (1978), Monroe (1968), Navarro, Peterson, Escalante & Benítez (1992), Orton (1871), Phillips (1962), Remsen, Traylor & Parkes (1986), Ridgely & Gwynne (1989), Ridgway (1911), Rowley (1966, 1984), Salaman & Gandy (1994), Sick (1993, 1997), Slud (1964), Snow (1962a), Snow & Snow (1964), Snyder (1966), Stiles & Negret (1994), Stiles & Skutch (1989), Stotz *et al.* (1996), Vallety & Avers (1997), Wendelken & Martin (1986), Wetmore (1968a), Whitacre (1989), Whitney *et al.* (1994).

2. Tepui Swift

Cypseloides phelpsi

French: Martinet des tépui German: Phelpssegler Spanish: Vencejo de Tepui
Other common names: Phelps's Swift

Taxonomy. *Cypseloides phelpsi* Collins, 1972, Cerro Auyan-tepui, Bolívar, Venezuela.

Forms superspecies with *C. rutilus*. It has recently been suggested that these two species should be included in *Streptoprocne* due to similarities in clutch size, development of young, and plumage, and these details would certainly suggest a close link with that genus. Monotypic.

Distribution. S Venezuela (Amazonas, Bolívar), NW Guyana (Merume Mts) and mountains of Brazilian border with Venezuela (NE Roraima).



Descriptive notes. 16.5 cm; male 20-23 g, female 19-23 g. Medium-sized swift with stocky body, long, relatively broad wings, and broad, moderately forked tail, deeper than *C. rutilus*; very black plumage with bright orange throat and collar. Female has paler orange collar and throat. Juvenile has shallower tail-fork and prominent pale fringing across whole underparts. **Habitat.** Main habitats have been defined as montane evergreen forest, tropical lowland evergreen forest and low, seasonally wet grassland. Recorded within breeding range at 400-1400 m, and from 1100 m as a vagrant. Often recorded in mixed flocks with *Streptoprocne zonaris*.

Food and Feeding. Not known.

Breeding. Late spring to early summer breeding season has been postulated. Recorded nest is truncated cone consisting of live moss sited on vertical wall, 1.5 m above floor, of small cave among boulders at edge of small stream.

Movements. Resident in Pantepui. Record from Aragua, N Venezuela, suggests some degree of dispersal.

Status and Conservation. Not globally threatened. Restricted-range species: present in Cordillera de la Costa Central EBA and Tepuis EBA. Commonly encountered in Venezuela in Cerro Tamacuari region (Amazonas); also regularly recorded at La Escalera (Bolívar).

Bibliography. Barrowclough, Escalante *et al.* (1995), Barrowclough, Lenino & Sweet (1997), Collins (1972a), Dickerman & Phelps (1982), Gilliard (1941), Meyer de Schauensee & Phelps (1978), Navarro, Peterson, Escalante & Benítez (1992), Sick (1993, 1997), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Whitacre (1989), Willard *et al.* (1991).

3. Black Swift

Cypseloides niger

French: Martinet sombre German: Schwarzsegler Spanish: Vencejo Negro

Taxonomy. *Hirundo nigra* J. F. Gmelin, 1789, Hispaniola.

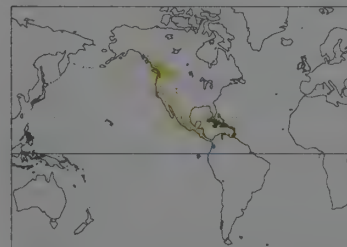
Previously placed in genus *Nephocetes*. Forms superspecies with *C. lemosi*, *C. rothschildi* and *C. fumigatus*. Darkness of plumage varies within range of nominate; proposed race *jamaicensis*, from S West Indies, now considered synonymous with nominate. Three subspecies currently recognized.

Subspecies and Distribution.

C. n. borealis (Kennerly, 1858) - W North America S to SW USA; winters in South America.

C. n. costaricensis Ridgway, 1910 - C Mexico S to Costa Rica; winters S of Mexican Isthmus.

C. n. niger (J. F. Gmelin, 1789) - West Indies to Trinidad.



Descriptive notes. 18 cm; 35-45 g. Rather a large swift with shallow, though distinctly, forked tail; long, broad wings and stocky body; dark plumage with white fringes to underparts, though these are sometimes lacking. Female has broader white fringing to underparts. Juvenile shows broad, white, rather spotty fringes on underbody. Race *borealis* is larger with strikingly black plumage, notably paler, grey head, especially forehead, and more prominent white fringing on underparts; *costaricensis* is generally darker and smaller than *borealis*.

Habitat. Occurs mainly at 1200-3000 m in Mexico; breeds 555-1400 m in S California,

and from close to sea-level up to 2600 m in British Columbia. In West Indies prefers forested highlands. In continental N America occurs over variety of open highland habitats. Occasionally seen in lowlands. Post-breeding flocks occur up to 3350 m in C Sierra Nevada, California. Main Neotropical habitats defined as edge of montane evergreen forest and secondary forest.

Food and Feeding. Studies reveal Hymenoptera predominate in diet; 276 prey items from 2 adults consisted of 4 species of Hymenoptera, including 200 individuals of a species of winged ant. Diet provided by adults to young in British Columbia was dominated by ants (Formicidae), nestling stage being timed to coincide with swarms of flying ants. Rain in highlands can force feeding to occur in lowlands. Highly gregarious, sometimes in flocks numbering thousands. In some areas parents breeding in mountainous areas travel many kilometres to lowland feeding sites. Race *borealis* collected at 1800 m in S Colombia where it was feeding in mixed flocks with *Streptoprocne zonaris*, *C. rutilus*, *C. lemosi*, *C. cryptus* and *C. cherriei* on immense swarms of various small beetles during late Sept to early Oct.

Breeding. Collected in breeding condition Costa Rica May-Jul and Dominica Jun-Jul; mating Jun, Cascade Mts (SW Canada, NW USA), with breeding behaviour Jul to early Aug; eggs in British Columbia from late Jun, in California mid-Jun to late Jul (peaking end Jun to early Jul), and in Costa Rica late May; small colony in Veracruz, Mexico, had nests with nestlings Jul; active colonies in Colorado Jul-Aug; nests with young in Montana late Jul. Single-brooded. Nest-sites have 6

On following pages: 4. White-chested Swift (*Cypseloides lemosi*); 5. Rothschild's Swift (*Cypseloides rothschildi*); 6. Sooty Swift (*Cypseloides fumigatus*); 7. Spot-fronted Swift (*Cypseloides cherriei*); 8. White-chinned Swift (*Cypseloides cryptus*); 9. White-fronted Swift (*Cypseloides storeri*); 10. Great Dusky Swift (*Cypseloides senex*); 11. White-collared Swift (*Streptoprocne zonaris*); 12. Biscutate Swift (*Streptoprocne biscutate*); 13. White-naped Swift (*Streptoprocne semicollaris*).

requirements: most often high relief, water, inaccessibility, darkness, unobstructed flyway immediately in front, and rock niche to build nest on. In British Columbia, nests found on canyon walls near water, especially waterfalls; typically nests on rock ledge beneath overhanging moss. Nest a pad of moss with lesser amounts of twigs and pine needles, bound with mud; ferns and seaweed also used depending on availability. One nest measured 140 mm wide, 100 mm back to front and 20 mm deep. May copulate in flight. Clutch normally 1 egg, occasionally 2; no replacement laying, if egg lost; incubation 23-27 days; young fed once or twice daily, typically at dusk by each parent; fledging period c. 45 days with brood dates in British Columbia from mid-Jul to mid-Sept.

Movements. Definite wintering grounds for any race uncertain. May be resident in Greater Antilles, though breeding visitor only to Puerto Rico from late Mar to mid-Aug. Present in Lesser Antilles from Mar/Apr to Aug/Sept. Records in Jun from Guyana and in Jul from Trinidad apparently contradict theory that nominate race winters in Guyana. Absent in winter from Costa Rica, no certain records Nov-Mar, and majority, at least, leave Mexico N of Isthmus from Oct to Feb. Race *borealis* now known to winter somewhere in South America, as recorded late Sept to early Oct in Cauca, S Colombia. Migration from Central America to South America may be in part over Pacific, records offshore including 135 km off Guatemala's Pacific coast. Main spring arrivals: S California mid-May, British Columbia mid-late May to Jun. Main return migration: British Columbia late Aug to mid-Sept, S California late Aug to Oct. Rarely recorded from SE Farallon Is (42 km W of San Francisco) mid-Jun and early Aug to early Oct. Race *borealis* occurs on Mexican Pacific slope Apr-May and Aug-Sept and offshore from Baja California S. Migration may occur Costa Rica Apr to early May and Sept to early Oct. Often migrates in large flocks, with groups of 300-400 noted during spring migration in California. Summer escape movements associated with passage of cyclones in British Columbia. Vagrant to E USA N to Massachusetts.

Status and Conservation. Not globally threatened. Abundance varies throughout range. Locally frequent to common in Mexico, rare and very localized in California, fairly common to locally very abundant in coastal British Columbia. Recent survey work revealed a significant downward trend (-9.1% p.a.) in Canadian population over 1966-1995, though an apparently larger significant upward trend (+24.3% p.a.) in US numbers during 1980-1995. Estimated S Californian population in 1985 and 1986 was 28 and 26 adults respectively, though largest Californian colony more recently has held over 20 pairs. High breeding success noted in this population; small numbers apparently due to lack of suitable nesting sites.

Bibliography. Amos (1991), Baicich & Harrison (1997), Beebe (1959), Bent (1940), Biaggi (1983), Binford (1989), Boad (1941, 1956a), Buchanan & Fierstine (1964), Campbell *et al.* (1990), Collins & Foerster (1995), Collins & Landy (1968), Davidson (1934), Davis (1964), Dawson (1915), DeGraaf & Rappole (1995), Dixon (1935), Dod (1987), Drew (1882), Dunn (1979), Eisenmann & Lehmann (1962), Erickson *et al.* (1989), Fix (1988), Foerster (1987), Foerster & Collins (1990), Grant, J. (1966), Griscom (1924), Hall (1948), Herklots (1961), Holroyd & Holroyd (1987), Holroyd & Jalkotzy (1986), Holroyd & Ulrich (1993), Howell & Webb (1994, 1995a), Howell *et al.* (1997), Hunter & Baldwin (1962), Jobin (1952), Kaufman (1996), Keith (1997), Kepler (1972), Kiff (1975), Knorr (1950, 1961, 1962, 1993a, 1993b), Knorr & Knorr (1989), Kondla (1973), Lee *et al.* (1996), Legg (1956), Marin (1997b, 1997c), Marin & Sánchez (1998), Marin & Stiles (1992), Michael, C.W. (1927), Michael, E. (1926), Monroe (1968), Murphy (1951), Navarro, Peterson, Escalante & Benítez (1992), Pyle & Henderson (1991), Raffaele (1989), Raffaele *et al.* (1998), Rathbun (1925), Ridgely & Gwynne (1989), Ridgway (1910, 1911), Righter (1994), Slud (1964), Small (1994), Smith (1928), Stiles & Negret (1994), Stiles & Skutch (1989), Stotz *et al.* (1996), Udvary (1954), Unitt (1981), Versaw (1996), Vrooman (1901, 1905), Webster (1958), Wetmore & Swales (1931), Weydemeyer (1975), Whitacre (1989), Zimmer (1945b).

4. White-chested Swift

Cypseloides lemosi

French: Martinet à plastron blanc **German:** Brustflecksegler **Spanish:** Vencejo Pechiblanco
Other common names: Giant Swift

Taxonomy. *Cypseloides lemosi* Eisenmann and Lehmann, 1962, Santander, Colombia. Previously placed in genus *Nephaocetes*. Forms superspecies with *C. niger*, *C. rothschildi* and *C. fumigatus*. Monotypic.

Distribution. SW Colombia in upper Cauca Valley, departments of Valle and Cauca. Also recently recorded in NC Colombia, NE Ecuador and NW Peru.



Descriptive notes. 14 cm; 29 g. A medium-sized swift with long, broad wings and a distinctly forked tail; blackish plumage, especially upperparts where forehead only slightly paler, with diagnostic white chest patch. Female has shallower tail-fork; chest patch reduced, or sometimes even missing; variable extents of pale fringing on underparts. Juvenile similar to female but with shallower tail-fork.

Habitat. All previous records, including tentative Ecuadorian sightings, were at 1050-1300 m, but species recently seen at 1800 m in Cauca, C Andean foothills, foraging over undulating plain cut through by R Blanco and R Cauca. Collected over highly eroded grassy hills with sparse scrubby cover. Seen once over level pasture. Main habitats defined as secondary forest and second-growth scrub.

Food and Feeding. Observed in, and collected from, either monospecific flocks or flocks including *C. rutilus*, *C. cryptus* or *Streptoprocne zonaris*. All published Colombian records of flocks have been of 20-25 birds. First of recent probable records from Ecuador was of 2 seen in flock of c. 150 *Cypseloides* swifts feeding in early morning at elevation of 50-100 m. Recently observed feeding in mixed flocks with *Streptoprocne zonaris*, *C. rutilus*, *C. niger borealis*, *C. cryptus* and *C. cherriei* on immense swarms of various small beetles during late Sept to early Oct in S Colombia.

Breeding. Not known.

Movements. Recorded in range from Feb to May and Oct and suspected to be resident.

Status and Conservation. **VULNERABLE.** Restricted-range species; present in Colombian Inter-Andean Valleys EBA. Known from only a handful of specimens and field sightings. Located near Cerro Munchique in 1962, and again more recently, and a population may persist there. Recently recorded from several new sites, where status remains unclear: 12 birds at Río Suárez, NC Colombia, in 1989; probable records from Napo Province, NE Ecuador; and first Peruvian record, Cordillera del Condor, NW Peru. Very little known of species' ecological requirements; until this lack of data has been rectified, effect of expanding area of eroded habitat within range will remain unknown. It has been suggested that use of agrochemicals may be affecting populations.

Bibliography. Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Eisenmann & Lehmann (1962), Hilty & Brown (1986), Meyer de Schauensee (1982), Navarro, Peterson, Escalante

& Benítez (1992), Olrog (1968), Schulenberg & Awbrey (1997), Stattersfield *et al.* (1998), Stiles & Negret (1994), Stotz *et al.* (1996), Wege & Long (1995).

5. Rothschild's Swift

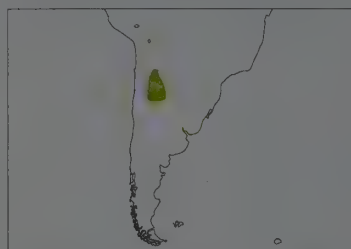
Cypseloides rothschildi

French: Martinet de Rothschild **German:** Rothschildsegler **Spanish:** Vencejo Parduzco
Other common names: Giant/Great Swift

Taxonomy. *Cypseloides rothschildi* Zimmer, 1945, Tucumán, Argentina.

Forms superspecies with *C. niger*, *C. lemosi* and *C. fumigatus*. Sometimes considered conspecific with *C. fumigatus*, and possibly *C. cryptus*. Older name for species, "*C. major*", is preoccupied by a synonym of *C. senex*. Monotypic.

Distribution. NW Argentina, in Salta, Tucumán and Santiago del Estero. Speculated to occur in Bolivia and Peru; single record from Cuzco, Peru.



Descriptive notes. 15 cm. A medium-sized swift with long, broad wings and a short, rather square tail; very uniform mid-brown all over. In the hand, separable from *C. fumigatus* by soft tail, which lacks stiffened or protruding father shafts; paler plumage and longer wings on average.

Habitat. In general, not very well known. Species is believed to occur exclusively within an altitude range of 500-2000 m. A flock of swifts, believed to be of present species, was recorded over an arid intermontane valley at 1500 m in W Santa Cruz, Bolivia. Main habitat has been defined as montane evergreen forest.

Food and Feeding. No information available.

Breeding. No information.

Movements. Resident. It has been suggested that Cuzco record does not refer to dispersal or vagrancy but that species' range includes Peru, but others believe it may winter N to Bolivia and Peru. A flock, c. 30, possibly of this species was recorded in Santa Cruz, Bolivia, in mid-Mar.

Status and Conservation. Not globally threatened. Currently considered Near-threatened. Restricted-range species; present in Argentina and South Bolivian Yungas EBA. No precise information regarding population size or trends. Species can sometimes be seen along road between Salta and Humahuaca, Argentina.

Bibliography. Canevari *et al.* (1991), Collar *et al.* (1994), Eisenmann & Lehmann (1962), Fjeldså & Mayer (1996), Narosky & Yzurieta (1993), Navarro, Peterson, Escalante & Benítez (1992), Nore & Salvador (1985), Olrog (1963a), de la Peña (1994), Remsen & Ridgely (1980), Short (1975), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Zimmer (1945b, 1953b).

6. Sooty Swift

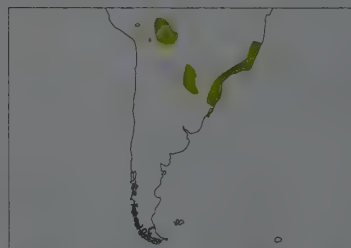
Cypseloides fumigatus

French: Martinet fuligineux **German:** Rauchsegler **Spanish:** Vencejo Negruczo

Taxonomy. *Hemiprocne fumigata* Streubel, 1848, Brazil.

Forms superspecies with *C. niger*, *C. lemosi* and *C. rothschildi*. Sometimes considered conspecific with *C. rothschildi*, and possibly *C. cryptus*. Monotypic.

Distribution. E Bolivia (Santa Cruz) through E Paraguay (Oriente) and extreme NW Argentina (Misiones) to SE Brazil (Espírito Santo S to Rio Grande do Sul).



Descriptive notes. 15 cm; 44 g. A medium-sized swift with a short, square tail and rather long wings; plumage generally sooty black-brown all over, with a tendency towards a paler forehead.

Habitat. Main habitats have been defined as montane evergreen forest, tropical lowland evergreen forest, southern temperate forest and second-growth scrub. Recorded at 700-2100 m. Closely associated with waterfalls and could be found over any nearby habitat within range.

Food and Feeding. Species has usually noted foraging in small groups of 3-6 birds, and has

been seen in association with *Chaetura* and *Streptoprocne* swifts. Up to 100 individuals noted at a single roost in Paraguay.

Breeding. Collected in breeding condition Rio Grande do Sul in early Oct and early Nov. Nests on canyon walls. Nest is conical structure of moss, pebbles and mud, lined with ferns. One egg.

Movements. Resident. Observations suggest that in Oriente, Paraguay, it may be partially migratory, with influx of birds in spring.

Status and Conservation. Not globally threatened. Probably commoner than previously supposed, as a result of identification difficulties. Scarce resident in E Paraguay, though regular at Aguara Nu, Mbaracayú Forest Nature Reserve, where population apparently swells with arrival of spring migrants. Not uncommon in NW Argentina and SE Brazil; range could extend through regions of S Brazil between mapped areas. Occurs in Serra dos Orgãos, Itatiaia and Aparados da Serra National Parks, Brazil.

Bibliography. Anon. (1993a), Belton (1984), Brooks, Barnes *et al.* (1993), Brooks, Clay *et al.* (1995), Canevari *et al.* (1991), Chebez (1994), Clay *et al.* (1998), Dabbene (1981), Eisenmann & Lehmann (1962), Hayes (1995), Lowen, Bartrina, Clay & Tobias (1996), Lowen, Clay *et al.* (1997), Narosky & Yzurieta (1993), Navarro, Peterson, Escalante & Benítez (1992), Olrog (1979b), Pacheco *et al.* (1996), Reboratti (1918), do Rosário (1996), Sick (1993, 1997), Stotz *et al.* (1996), Tobias *et al.* (1993), Whitacre (1989), Zimmer (1945b).

7. Spot-fronted Swift

Cypseloides cherriei

French: Martinet à points blancs **German:** Diademsegler **Spanish:** Vencejo Cuatro-ojos
Other common names: Cherrie's Swift

Taxonomy. *Cypseloides cherriei* Ridgway, 1893, Volcán de Irazú, Costa Rica.

Monotypic.

Distribution. Scattered and poorly known: Costa Rica (Cordillera Central on Pacific slope); N Venezuela (Aragua, coastal cordillera); NC & SW Colombia (San Gil, Santander; Changuayaco by Cerro Munchique and Las Guacas near Popayán, in W Andes of Cauca) and N Ecuador (Pichincha, W slope of Andes).



Descriptive notes. 14 cm; 23 g. Small swift with short square tail and relatively short wings; blackish plumage with striking head pattern; white supraloral patch, post-ocular streak and pale fringes over eye-patch. Browner individuals may be first-summer or have retained juvenile plumage. Juvenile as fresh adult but fringing on underbody broader, remiges narrowly fringed greyish white, and post-ocular spot smaller.

Habitat. Not recorded outside mountainous areas; all localities 1100–2200 m. Main habitat defined as montane evergreen forest. Occurs in forested uplands with deep valleys. In Costa

Rica especially favours deep gorges; also recorded foraging over brushy savanna at Helecheles. **Food and Feeding.** Of 719 prey items analysed, from 2 boluses and 2 stomachs, 87% were Hymenoptera and Hemiptera. In Costa Rica occurs singly or in pairs, often in association with *C. rutilus*. Tends to forage in higher strata of mixed swift flocks. A number have been recorded after sunset during thick fog, at Rancho Grande, Venezuela, where they were attracted to lights. It has been suggested that *Cypseloides* feed later than other sympatric genera and can experience problems reaching suitable roosting areas when caught in inclement weather. Recently observed feeding in mixed flocks with *Streptoprocne zonaris*, *C. rutilus*, *C. cryptus*, *C. lemosi* and *C. niger borealis* on immense swarms of various small beetles during late Sept to early Oct, in department of Cauca, Colombia.

Breeding. In Venezuela active nests recorded Jul–Aug; in Ecuador c. 18-day-old chick in nest in mid-Jun and hatching period for that country thought to be late Apr to early Jun; in Costa Rica egg-laying late May to mid-Jul, stimulated not by first rains of season but by heavier falls of May/June; strong nest-site fidelity. Widest variation in nest-site of all well-studied *Cypseloides*; form also differs with site type, though typically cupped or half-cupped depending on width and angle of support; nest 1–5 m above water; typically moderately to fully saturated, though some drier, consisting of mosses and liverworts with lining of dry bamboo leaves and ferns; where bryophytes not readily available coarse vegetable fibres employed to great extent in construction and as lining. Most substantial in wettest situations with greatest volume of mud in base, though normally less substantial with only bare minimum of material to form nest cup; typically on rock knob or narrow ledge sloping outwards at 45° and protected by overhang; mean height 56 mm, width 104 mm, front to back 68 mm, depression 18 mm deep × 64 mm wide × 40 mm front to back. Two nests in Ecuador were 3 m apart with Andean Cock-of-the-Rock (*Rupicola peruviana*) nest close by. Single egg; incubation period in Costa Rica 26–28 days; nestling period 65–70 days.

Movements. No indication of migratory behaviour.

Status and Conservation. Not globally threatened. Despite paucity of sightings, specimens and recorded localities, present species may prove to be more widespread and abundant than currently thought, though it certainly appears to be one of the rarer Neotropical swifts.

Bibliography. Beebe (1949), Chantler (1998), Collins (1967c, 1968b, 1980b), Hilty & Brown (1986), Kiff (1975), Marín (1993), Marín & Stiles (1992, 1993), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Navarro, Peterson, Escalante & Benítez (1992), Olog (1968), Slud (1964), Stiles & Negret (1994), Stiles & Skutch (1989), Stotz *et al.* (1996), Whitacre (1989), Zimmer (1945b).

8. White-chinned Swift

Cypseloides cryptus

French: Martinet à menton blanc **German:** Weißkinnssegler **Spanish:** Vencejo Barbiblanco
Other common names: Zimmer's Swift

Taxonomy. *Cypseloides cryptus* Zimmer, 1945, Inca Mine, Peru.

Forms superspecies with *C. storeri*, and the two are sometimes considered conspecific. Another proposal suggests that present species might be conspecific with *C. rothschildi* and *C. fumigatus*. Monotypic.

Distribution. Scattered and poorly known: in Central America, occurs primarily on Caribbean slope lowlands of Belize, Honduras, Nicaragua, Costa Rica and Panama; recorded from Andes and associated lowlands in Peru, Ecuador, Colombia and Venezuela; also cordilleras of N Venezuela, and tepuis of S Venezuela and Guyana.



Descriptive notes. 15 cm; 35 g. A medium-sized swift with a rather squat appearance and a relatively short, square tail; generally blackish with pale grey areas on chin, distal part of forehead, and lores, as well as line over eye, though this is very hard to see in field. Brown individuals, possibly still in juvenile plumage, have a reduced chin patch. Tail relatively shorter than in smaller *C. cherriei*.

Habitat. Main habitats defined as montane evergreen forest and tropical lowland evergreen forest. Prefers uplands with gorges and waterfalls, which it uses for both roosting and breeding. Taken at Helecheles, Costa Rica, between

1000–1500 m in habitat containing brushy savanna, some agriculture and humid primary forest. Occurs between sea-level and 3000 m.

Food and Feeding. Analysis of prey items from 4 stomachs and 2 boluses showed that 92% were Hymenoptera. Two females collected from N Venezuela contained many *Azteca* ants, and one of these also many *Crematogaster* ants. Less highly gregarious than other species, though often with other *Cypseloides* and *Streptoprocne* swifts and more occasionally other genera. Feeds in higher strata when foraging with other swift species. Recently seen feeding in mixed flocks with *Streptoprocne zonaris*, *C. rutilus*, *C. niger borealis*, *C. lemosi* and *C. cherriei* on immense swarms of various small beetles during late Sept to early Oct in S Colombia.

Breeding. In Costa Rica egg-laying from early May to early Jun prompted not by first rains of wet season but by heavier rains May–Jun; strong nest-site fidelity. Site closely associated with falling

water and typically protected by permanently wet *Pilea* sp., occasionally mosses or liverworts. Permanently saturated nest consists of mosses and liverworts with highest percentage of mud in base; shallow bowl or half-cup, mean measurements 76.5 mm front to back, 107 mm wide, 48 mm high; depression 49.5 mm front to back × 65.5 mm wide × 13.5 mm deep. Single egg; incubation period, Costa Rica, c. 30 days; nestling period 55–58 days.

Movements. Resident.

Status and Conservation. Not globally threatened. Generally uncommon, with rather scattered distribution, and definitely known from very few sites, e.g. in Colombia from Cauca and Córdoba, in Venezuela from Táchira, Aragua and Bolívar. At best-known breeding site in Costa Rica, low density of species is apparent.

Bibliography. Beebe (1947, 1949), Chantler (1998), Collins (1968b), Eisenmann & Lehmann (1962), Hilty & Brown (1986), Howell, S.N.G. & Webb (1995a), Howell, S.N.G., Dowell *et al.* (1992), Howell, S.N.G., Snetsinger & Wilson (1997), Howell, T.R. (1957), Kiff (1975), Marín (1993), Marín & Stiles (1992), Meyer de Schauensee & Phelps (1978), Monroe (1968), Navarro, Peterson, Escalante & Benítez (1992), Ridgely & Gwynne (1989), Slud (1964), Snyder (1966), Stiles & Negret (1994), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968a), Whitacre (1989), Zimmer (1945b).

9. White-fronted Swift

Cypseloides storeri

French: Martinet de Storer **German:** Weißstirnsegler **Spanish:** Vencejo Frentiblanco
Other common names: White-faced Swift

Taxonomy. *Cypseloides storeri* Navarro *et al.*, 1992, Puerto del Gallo, Guerrero, Mexico.

Forms superspecies with *C. cryptus*. Much debate surrounds status of this form (see page 416); considered a race of *C. cryptus* by some authorities. Monotypic.

Distribution. SW Mexico in mountains of Michoacan, Guerrero and Jalisco.



Descriptive notes. 14 cm; 39.5 g. Medium-sized swift with short square tail and squat body; sooty black-brown with greyish chin, lores and forehead. Structure and plumage very like *C. cryptus*; in hand, these two species may be identified by tail/tarsus ratio, present species 36.5 and *C. cryptus* 34–36; present species also differs from latter by whitish, not sooty, post-orbital feathers and more abruptly terminating face pattern.

Habitat. Collected at 1500–2500 m in forested areas with numerous waterfalls and ravines. Guerrero habitat classified as montane cloud-forest, whereas Michoacan forest where collection occurred is transitional between pine-oak and dry tropical deciduous. Possibly sighted with large numbers of *Streptoprocne semicollaris* and *C. rutilus* entering waterfall roost site. Probable individual observed at Tacambaro was seen flying over hills and fields cut through by a narrow steep-sided canyon at 1200 m.

Food and Feeding. Not known. A presumed individual of this species was observed in a flock of c. 100 swifts comprising 80–90 *C. rutilus*, 4 *C. niger* and 1 *Chaetura vauxi*.

Breeding. No information.

Movements. Lack of information makes migratory status equivocal. May be resident or breeding visitor during Jul–Sept, possibly May.

Status and Conservation. Not globally threatened. Data-deficient. Restricted-range species: present in Sierra Madre Occidental and Trans-Mexican Range EBA and Sierra Madre del Sur EBA. Known from only 5 specimens and 1 probable sight record. Lack of sightings of unidentified dark *Cypseloides* within range combined with paucity of museum specimens suggests rarity.

Bibliography. Anon. (1998a), Chantler (1998), Collar *et al.* (1994), Hernández-Baños *et al.* (1995), Howell (1993d), Howell & Webb (1995a), Howell *et al.* (1997), Navarro, Benítez *et al.* (1993), Navarro, Peterson, Escalante & Benítez (1992), Peterson & Navarro (1993), Stattersfield *et al.* (1998), Stotz *et al.* (1996).

10. Great Dusky Swift

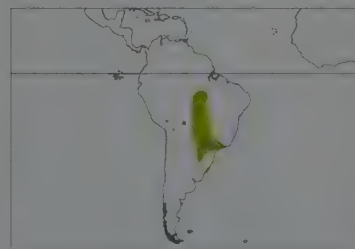
Cypseloides senex

French: Martinet à tête grise **German:** Rußsegler **Spanish:** Vencejo Canoso

Taxonomy. *Cypseloides senex* Temminck, 1826, Brazil.

Due to differences in tail and foot structure, species has been placed in genus *Aerornis*, either alone or with *Streptoprocne semicollaris*. Monotypic.

Distribution. C & S Brazil, E Paraguay (Oriente) and N Argentina (Misiones); may also breed in Serranía de Huanchaca, NE Bolivia, where recently recorded.



Descriptive notes. 18 cm; 60–98 g. Large swift with square or slightly rounded tail, long broad wings and bulky body; brown with paler head (forehead can appear quite whitish) and slightly paler rump. Juvenile has comparatively pale median primary coverts.

Habitat. Breeds and roosts around waterfalls, feeding over nearby habitats. Recorded from lowlands to 1000 m. Recent record from Bolivia was at 180 m altitude.

Food and Feeding. Feeds high over forest canopy during day. Gregarious, often associating with *S. zonaris*.

Breeding. Colonial, nesting on horizontal ledges adjacent to or behind waterfalls, often in direct sunlight. Nests are disc-shaped cones of moss and pebbles bound together with mud.

Movements. Equivocal migratory status. Generally believed to be resident. Some authors have suggested transequatorial migration on strength of “probable” sightings from Iquitos, Peru. Records from Bolivia in Noel Kempff Mercado National Park and Serranía de Huanchaca may refer to undiscovered breeding populations.

Status and Conservation. Not globally threatened. Generally common to locally abundant, though scarce to uncommon in Paraguay. Large numbers breed at Falls of Iguaçu, in area on Brazil–Argentina border; also present in several other protected areas, e.g. Noel Kempff Mercado National Park

(Bolivia), Ybicuí National Park and La Golondrina and Estancia Itabo Private Nature Reserves (Paraguay) and Serra da Canastra National Park (Brazil). Future of certain sites may be threatened by dam building.

Bibliography. Allen (1893), Brooks *et al.* (1993), Canevari *et al.* (1991), Chebez (1993b, 1994), Dubs (1992), Hayes (1995), Hayes & Scharf (1995a), Hilty & Brown (1986), Narosky & Yzurieta (1993), Navarro, Peterson, Escalante & Benítez (1992), de la Peña (1982, 1994), Saibene *et al.* (1996), Schubart *et al.* (1965), Sick (1993, 1997), Stotz *et al.* (1996), Whitacre (1989), Whitney *et al.* (1994), Zimmer (1945b).

Genus *STREPTOPROCNE* Oberholser, 1906

11. White-collared Swift

Streptoprocne zonaris

French: Martinet à collier blanc **German:** Halsbandsegler **Spanish:** Vencejo Acollarado
Other common names: Collared/Antillean Cloud/Giant White-collared/Ringed Swift

Taxonomy. *Hirundo zonaris* Shaw, 1796, Brazil.

Recent research has shown that race *albicincta* is far more restricted in range than previously thought. Nine subspecies recognized.

Subspecies and Distribution.

S. z. mexicana Ridgway, 1910 - S Mexico to Belize.

S. z. bouchellii Huber, 1923 - Nicaragua to Panama.

S. z. pallidifrons (Hartert, 1896) - Greater Antilles and locally in Lesser Antilles (Saba, Grenadines, Grenada).

S. z. minor (Lawrence, 1882) - Cordillera of coastal N Venezuela, recorded to Trinidad.

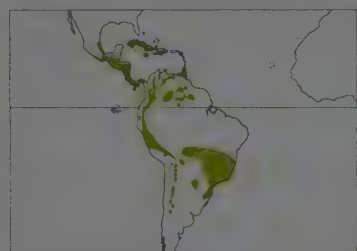
S. z. albicincta (Cabanis, 1862) - lowland Venezuela (S of Andes and cordilleras), Guyana and possibly Surinam and French Guiana.

S. z. subtropicalis Parkes, 1993 - middle elevations in Andean highlands from Mérida (Venezuela) and Colombia to Peru.

S. z. altissima Chapman, 1914 - high elevations of Andes in Colombia and Ecuador.

S. z. kuenzeli Niethammer, 1953 - high elevations of Bolivian Andes and NW Argentina.

S. z. zonaris (Shaw, 1796) - S Brazilian and Bolivian lowlands, and C & E Paraguay.



Descriptive notes. 22 cm; 104 g. Large swift with sturdy body, broad wings and shallowly forked tail; blackish plumage broken by distinctive white collar. Juvenile shows extensive white fringing to body feathers and mottled collar. Race *subtropicalis* is smaller and more deeply black, with broader white collar; *albicincta* is small, with broad breast band and restricted buff fringing; *mexicana* large with greyer underparts and broad breast band; *bouchellii* blacker than latter with narrower breast band; *minor* with narrow, often mottled, breast band and greyish throat; *pallidifrons* with face and sometimes throat contrastingly pale,

and buff-fringed marginal coverts, especially juvenile; *altissima* very large with very broad collar, black plumage, slightly paler throat and white-fringed marginal coverts; *kuenzeli* has brownish underparts and distinct pale fringing on marginal coverts and superciliary area.

Habitat. Within large range often montane or submontane, to 4350 m in Andes, and from sea-level to 2500 m in Mexico; breeds only on those Caribbean islands with terrain over 2000 m. However, does occur over variety of lowland and highland habitats, coastal and interior. Widest altitudinal range of any Ecuadorian swift: 300-4000 m, to 4200 m on E slope, equally abundant throughout. Main habitats defined as montane evergreen forest, tropical lowland evergreen forest, secondary forest and second-growth scrub. Least abundant in arid regions. Over open, scrubby habitat, Rio Negro Preserve, Costa Rica, and over broadleaved forest, pine ridge and savanna, Hill Bank, N Belize. During habitat study in Villavieja area, Colombia, found over wide range of habitats, including residential, with exception of rice fields.

Food and Feeding. Two digestive tracts obtained in Mexico contained 842 and 538 individual insects with 1 spider, Orders Hemiptera, Hymenoptera, Coleoptera, Lepidoptera and Diptera and suborder Homoptera were found in both tracts, and 811 and 471 of the prey items respectively were 1 ant species (*Azteca foreli*), indicating importance of swarming insects. Highly gregarious, often seen in large flocks with other swift genera. Frequently associates with *Chaetura vauxi* in Sierra de Tuxtla, Mexico, in flocks of 10-200. Forages daily over wide range, and localized weather-stimulated migrations are well established. Will feed low over cities if rain falling in typically favoured upland habitats nearby. Feeds higher than other swift species when present at same site in Ecuador.

Breeding. Adults in breeding condition, Rio Grande do Sul, early Oct; sexually active, Bolivia, Oct; eggs recorded in Ecuador, Jan; egg-laying begins in Costa Rica mid-Apr, peaking late Apr and finished by mid-May, probably stimulated by first rains; egg-laying at Mexican colony, early May; pullus recorded Tolima, Colombia, Apr and Venezuelan Andes, May-Jun. In Costa Rica nest-building starts in dry season. Nests singly or in colonies of up to 12 pairs. Nest-sites require darkness and solid, more or less horizontal, surface, typically caves next to or behind waterfalls; caves vary in size up to 1 m wide at entrance and several metres deep, entrances often screened by vegetation; often nests in spray of falling water. Typical nests are disc-shaped pads with shallow central depression, of mud and vegetable matter, mainly rootlets, mosses and liverworts, sometimes lined with vegetable fibres, fine mosses or even dry leaves; nest base typically wet, upper nest moist; occasionally no nest structure employed and eggs laid directly onto substrate; mean height 95 mm, central depression mean width 147 mm, depth 10 mm. Two eggs; incubation period c. 30-35 days; chicks apparently fed only once per day; nestling period c. 45-55 days.

Movements. Partly migratory, with various forms of dispersal in different populations. Some altitudinal dispersal into lowlands from Andean populations, May-Aug, in Peru. Noted in so-called "fire-following" movements, i.e. systematic exploitation of seasonal savanna fires in campo regions of South America. Chaco habitats in Bolivia used by non-breeding birds. Status in Argentina away from Andean breeding range of *kuenzeli* uncertain: may occur across N Argentina outside breeding season. Rare visitor to Grenada, May-Oct. Known to occur in S Petén, Guatemala, only in winter. Irregular visitor to Mexico N to Colima and Jalisco, Dec-Mar. Recorded in USA from California to Florida.

Status and Conservation. Not globally threatened. Locally common to abundant throughout much of extensive range, though race *pallidifrons* of West Indies scarce in parts, and species rare in some areas of Central America, especially on Pacific coast; extremely rare in N Belize, though abundant in suitable habitat in Costa Rica; uncommon in some parts of Andes. Occurs in numerous protected areas throughout extensive range, e.g. Braulio Carrillo, Volcán Irazú and Volcán Poás National Parks and Monteverde Biological Reserve (Costa Rica), Río Nambi National Reserve (Colombia), and Serra dos Órgãos and Itatiaia National Parks (Brazil); also in Ybicuí National Park (Paraguay), where uncommon.

Bibliography. Andrie (1967), Barbour (1943), Beavers *et al.* (1991), Becker & López (1997), Beebe (1947), Belton (1984), Best & Clarke (1991), Best *et al.* (1993), Binford (1989), Bloch *et al.* (1991), Canevari *et al.* (1991), Contreras *et al.* (1990), Cooper (1997), Cuello & Gerzenstein (1962), Erickson *et al.* (1989), Fjeldså & Krabbe (1990), Gardner (1972), Garrido & de la Cruz (1990), Hardy & Clench (1982), Haverschmidt & Mees (1994), Hayes (1995), Herklots (1961), Hilty & Brown (1986), Howell (1993b), Howell & Webb (1994, 1995a), Johnson (1967), Kepler (1972), Kirwan (1996b, 1996c), Krabbe & Sornoza (1994), Kratter *et al.* (1993), Lasley (1984), Lee *et al.* (1996), Marín (1993), Marín & Carrión (1994), Marín & Stiles (1992), McKay (1980), Meyer de Schauensee & Phelps (1978), Monroe (1968), Munves (1975), Nellar (1993), Parkes (1993), de la Peña (1982, 1994), Peres & Whittaker (1991), Raffaele *et al.* (1998), Remsen, Traylor & Parkes (1986), Ridgely & Gaulin (1980), Ridgely & Gwynne (1989), Ridgway (1910, 1911), Rogers (1939a), do Rosário (1996), Rowley & Orr (1962, 1965), Russell (1964), Saibene *et al.* (1996), Salaman & Gandy (1994), Sick (1948c, 1993, 1997), Slud (1964), Snow (1962a), Snyder (1966), Stiles & Skutch (1989), Stotz *et al.* (1996), Thomas (1993), Turner (1981), Valley & Whitman (1997), Wetmore (1957a, 1968a), Wetmore & Swales (1931), Whitacre (1989, 1992), Whitacre & Ukrain (1982), Zimmer (1945, 1953b).

12. Biscutate Swift

Streptoprocne biscutate

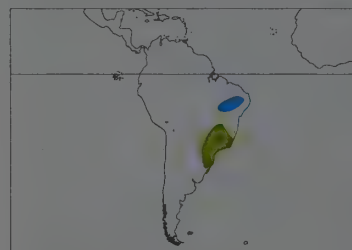
French: Martinet à collier interrompu **Spanish:** Vencejo Nuquiblanco Brasileño
German: Schildsegler

Taxonomy. *Chaetura biscutate* P. L. Sclater, 1865, Rio de Janeiro and Ypanema, São Paulo, Brazil. Two subspecies recognized.

Subspecies and Distribution.

S. b. seridoensis Sick, 1991 - Seridó, NE Brazil.

S. b. biscutate (P. L. Sclater, 1865) - Minas Gerais S to Rio Grande do Sul, E Brazil; also recorded in Paraguay and N Argentina.



Descriptive notes. 22 cm; 85-100 g. Large swift with long broad wings, sturdy body and square tail; black-brown with white nape and white upper-breast patches; paler fore-face and sometimes throat. Grey-white fringing to plumage in adult. Race *seridoensis* smaller than nominate.

Habitat. Main habitats have been defined as tropical lowland evergreen forest, montane evergreen forest, southern temperate forest, second-growth scrub and tropical deciduous forest. Roosts and breeds in dry caverns; foraging noted around waterfalls. Occurs between lowlands and c. 2500 m; breeds at 1600 m in

Ibitipoca Park.

Food and Feeding. Highly gregarious, frequently feeding in numbers around waterfalls. Where sympatric with *S. zonaris*, such as Itatiaia Mts, Rio de Janeiro, the two species do not readily associate.

Breeding. Season in Minas Gerais, Oct-Dec; birds in breeding condition, Rio Grande do Sul, early Oct. Nests on horizontal ledges in large dry caverns; nest is shallow, bowl-shaped disc of lichens, mosses and dry leaves.

Movements. Not fully understood. Breeding areas of Seridó roosting population (*seridoensis*) undiscovered. Nominate race arrives Minas Gerais from Aug, with some still present Feb, but wintering grounds unknown; possibly a transequatorial migrant.

Status and Conservation. Not globally threatened, though it has been suggested that population requires monitoring. Common to abundant, Rio Grande do Sul. At Seridó, 90,000-100,000 roosted at 1 cave at Serra do Bico da Arara in Aug 1978, and 1200 were reported roosting in 15 caves in 1984. Occurs in Chapada dos Guimarães and Aparados da Serra National Parks (Brazil). First record for Paraguay from Aguaraçu, Nov 1997.

Bibliography. de Andrade *et al.* (1985), Belton (1984), Canevari *et al.* (1991), Chebez (1994), Clay *et al.* (1998), Erickson *et al.* (1989), Hilty & Brown (1986), Norez & Yzurieta (1985), Olrog (1979b), Pacheco *et al.* (1996), do Rosário (1996), Saibene *et al.* (1996), Sick (1991, 1993, 1997), Stotz *et al.* (1996), Whitacre (1989).

13. White-naped Swift

Streptoprocne semicollaris

French: Martinet à nuque blanche **Spanish:** Vencejo Nuquiblanco Mexicano
German: Weißbackensegler

Taxonomy. *Acanthylis semicollaris* DeSaussure, 1859, San Joaquín, near Mexico City.

Previously placed in monospecific genus *Semicollum*, largely on the basis of nesting behaviour, but recent research has invalidated this opinion. Alternatively, has at times been linked with *Cypseloides senex* in genus *Aerornis*. Monotypic.



Distribution. W Mexico, in highlands of Chihuahua, Sinaloa, Nayarit, Hidalgo, Morelos and México.

Descriptive notes. 22 cm. Very large swift with heavy body, long broad wings and large square tail, appearing more rounded when fully spread; black-brown with distinct white nape patch. Juvenile probably has pale-fringed plumage and reduced nape patch.

Habitat. Essentially montane, mainly in arid inland regions where recorded to 3600 m. In Mexico at 1500-3000 m, though to sea-level in NW. Main habitats defined as pine-oak forest, tropical deciduous forest and second-

growth scrub. On occasions occurs to sea-level and also in small numbers over coastal slopes of Sierra Madre del Sur. Typically around deep gorges, cliffs and high crags, over forested slopes and brushlands, though also recorded over towns.

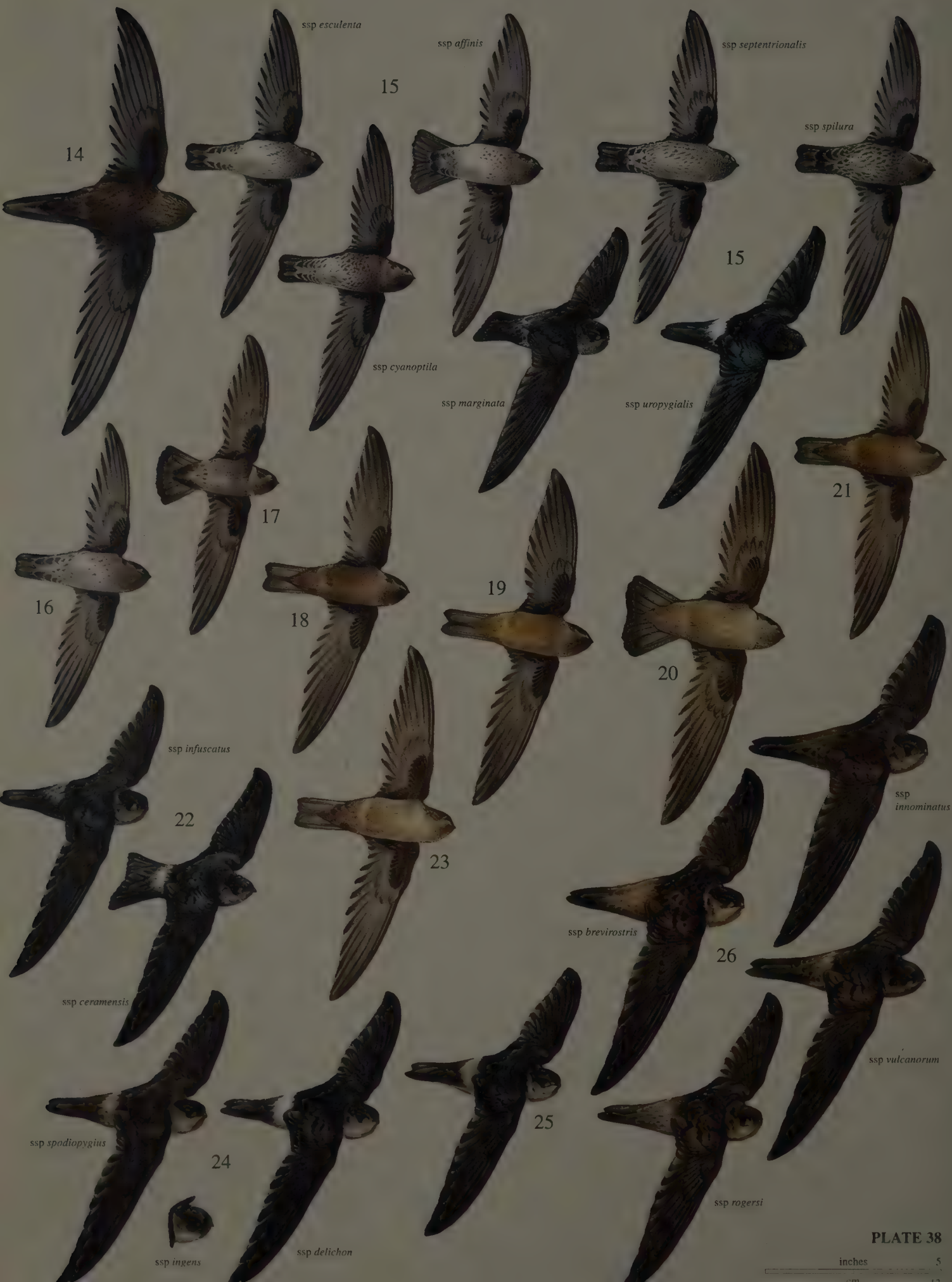
Food and Feeding. Upper portion of digestive tract of 1 specimen contained 1072 individual insects: 683 Hymenoptera, 391 Homoptera, 20 Hemiptera, 6 Diptera and 2 Coleoptera. Presence of 681 fire ants (*Solenopsis geminata*) illustrates importance of swarming insects.

Breeding. Eggs present in nests studied in late May. Nests colonially in caves mostly on solid, more or less horizontal, substrates; colonies up to 12 pairs recorded. Nest structure not always employed, with eggs laid in shallow, purpose-built depression, though 26 of 32 nests recently studied were structures mainly of mud with considerable plant material, circular or 40-75% circular truncating towards substrate slope; most nests lined with plant matter. Two eggs; chicks apparently fed only once per day.

Movements. Previously regarded as strictly resident. In Mexico, some withdraw from high cold altitudes in winter, as absent from Distrito Federal, Aug-Mar. Records from outside normal range in Chiapas, S Mexico, and flocks recorded in Apr-May 1993 in Belize suggest some form of dispersal.

Status and Conservation. Not globally threatened. Fairly common to locally common. Apparent break in range between the two main distributional blocks may reflect lack of suitable nesting and/or roosting areas. Regularly recorded at a number of sites, e.g. San Blas (Nayarit), Coajomulco and Cañón de Lobos (Morelos), Temascaltepec (México), Tacámbaro (Michoacan) and Sierra de Atoyac (Guerrero).

Bibliography. Anon. (1998a), Hernández-Baños *et al.* (1995), Howell (1993b), Howell & Webb (1994, 1995a), Land (1970), Mallory (1994), Monroe (1968), Ridgway (1911), Rowley & Orr (1962), Stotz *et al.* (1996), Whitacre (1989, 1992), Wilson & Ceballos-Lascurain (1993).



ssp esculenta

ssp affinis

ssp septentrionalis

ssp spilura

ssp cyanoptila

ssp marginata

ssp uropygialis

ssp infuscatus

ssp innominatus

ssp brevirostris

ssp vulcanorum

ssp ceramensis

ssp spodiopygius

ssp ingens

ssp delichon

ssp rogersi

PLATE 38

inches 5

cm 12

Subfamily APODINAE

Tribe COLLOCALIINI

Genus *HYDROCHOUS* Brooke, 1970

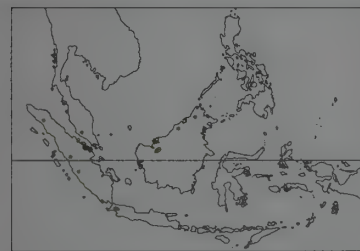
14. Waterfall Swift

Hydrochous gigas

French: Salangane géante **German:** Riesensalangane **Spanish:** Salangana Gigante
Other common names: Giant Swiftlet

Taxonomy. *Collocalia gigas* Hartert and Butler, 1901, Semangko Pass, Selangor, Malaysia. Genus possibly closest to *Aerodramus*, and these two commonly merged into *Collocalia*; however, large size and differences in breeding biology favour isolation of present species, although some researchers have considered these differences marginal and of doubtful taxonomic significance; other opinions suggest present species may not be closely related to the swiftlet genera. Monotypic.

Distribution. Mountainous areas of Peninsular Malaysia, Sumatra, Borneo and W Java.



Descriptive notes. 16 cm; male 37 g, female 35–39 g. A fairly large swift, appearing rather more like some of the Apodini swifts than the swiftlets, with deeply forked tail; uniformly dark brown above, slightly paler but still very uniform below. Not capable of echolocation.

Habitat. Typically found over mountainous rainforest in areas of waterfalls; known from c. 800 m in Malay Peninsula, c. 440 m in Sumatra and c. 300–1500 m in W Java.

Food and Feeding. Analyses of stomach contents from W Java show prey variable, presumably depending on availability: one stomach contained mainly flying ants, lesser numbers

of Diptera, including sizeable tipulid, a small beetle and a small bug. Others recorded predominance of Diptera. Believed to feed at times on winged termites. Gregarious, often with *Hirundapus giganteus* and to lesser extent *Collocalia linchi* on Java. Though lacks ability to echolocate, has acute poor-light vision and may be mainly a crepuscular feeder. Data suggest this species more likely to be seen foraging during day on Java in rainy season, Oct–Mar.

Breeding. Recorded Oct–Jan in W Java; egg taken late Apr in Malay Peninsula. Nest in latter location of liverworts, collected by birds by pulling with beak while still in flight, and to lesser extent mosses agglutinated with feathers and saliva into truncated cone and attached with same adhesive to rock substrate, on small ledge within spray of waterfall; 90 mm high with depression 12 mm deep × 37 mm wide. Clutch typically 1 egg.

Movements. Believed to be resident, though equivocal. Recorded at night from Fraser's Hill, W Malaysia, and on offshore islands, N Borneo.

Status and Conservation. Not globally threatened. Currently considered near-threatened. Restricted-range species; present in Sumatra and Peninsular Malaysia EBA and Bali Forests EBA. Rare and local, though exact status unclear with few population counts: 60–80 together at well-known breeding site (Gunung-Gede/Pangrango National Park) in W Java, Aug 1985. Counts of up to 8 at site near Gunung Kerinci, in Kerinci-Seblat National Park, SC Sumatra. Said to be common around Mt Pangrango in early 20th century. May be more widespread in Sumatra than currently thought, as 2 records (groups of 7 and 8) from Gunung Leuser and record of 2 from Brestagi. Distribution in Borneo similarly may be more extensive than currently thought. Recorded in Panti Forest Reserve, Johor Province, Malaysia, in Nov 1996.

Bibliography. Andrew (1985), Bartels (1915), Becking (1971), Clayton *et al.* (1996), Collar & Andrew (1988), Collar *et al.* (1994), Cranbrook (1984), Hellebrekers & Hoogerwerf (1967), Higgins *et al.* (1989), Holmes (1996), Hoogerwerf (1949a, 1949b), Inskipp *et al.* (1996), King (1987), Lee *et al.* (1996), MacKinnon (1988), MacKinnon & Phillips (1993), van Marle & Voous (1988), Medway (1966), Medway & Pye (1977), Medway & Wells (1969, 1976), Robson (1997b), Salomonsen (1983), Smythies (1981), Somadikarta (1968), Stattersfield *et al.* (1998), Tobias & Phelps (1994), Vowles & Vowles (1984), Wells (1992, 1999).

Genus *COLLOCALIA* G. R. Gray, 1840

15. Glossy Swiftlet

Collocalia esculenta

French: Salangane soyeuse **German:** Glanzkopfsalangane **Spanish:** Salangana Lustrosa
Other common names: White-bellied Swiftlet; Beavan's Swiftlet (*affinis*); Philippine(!)/Grey-rumped(!) Swiftlet (*marginata*)

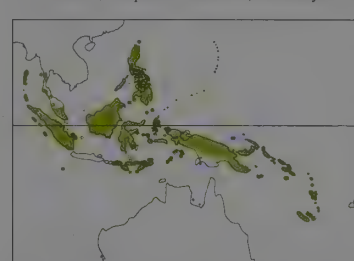
Taxonomy. *Hirundo esculenta* Linnaeus, 1758. China; error = Ambon.

May be conspecific with *C. linchi*; some authors place race *natalis* in *C. linchi*. Philippine birds commonly split off as a separate allospecies, *C. marginata*, largely on basis of grey rump. Much of variation appears to be clinal. Birds from Halmahera sometimes separated as race *nubila*, but this is

best considered a synonym of *spilura*. Populations on Salayar I and in Tanimbar Is are not currently assigned to any given subspecies; birds from Palawan and Calauit, tentatively placed in *marginata*, may belong to an undescribed race. First six races listed have been considered to form a distinctive western subgroup. Thirty-two subspecies recognized.

Subspecies and Distribution.

- C. e. affinis* Beavan, 1867 - Andaman and Nicobar Is.
- C. e. elachyptera* Oberholser, 1906 - Mergui Archipelago (Myanmar).
- C. e. cyanoptila* Oberholser, 1906 - Malay Peninsula, Sumatra and most of its satellites, and lowland Borneo.
- C. e. vanderbilti* Meyer de Schauensee & Ripley, 1941 - Nias I (off W Sumatra).
- C. e. oberholseri* Stresemann, 1912 - Batu Is and Mentawai Is (off W Sumatra).
- C. e. natalis* Lister, 1889 - Christmas I (Indian Ocean).
- C. e. septentrionalis* Mayr, 1945 - Babuyan, Calayan and N Camiguin Is (N Philippines).
- C. e. isonota* Oberholser, 1906 - N Luzon (N Philippines).
- C. e. marginata* Salvadori, 1882 - C Luzon S to Palawan and Bohol (W & N Philippines).
- C. e. bagobo* Hachisuka, 1930 - Mindoro, Mindanao and Sulu Archipelago (S Philippines).
- C. e. spilura* G. R. Gray, 1866 - N Moluccas.
- C. e. manadensis* Salomonsen, 1983 - N Sulawesi to Sangihe and Talaud Is.
- C. e. esculenta* (Linnaeus, 1758) - C & S Sulawesi through Banggai and Sula Is to C & S Moluccas.
- C. e. minuta* Stresemann, 1925 - Tanahjampea I and Kalao I, in N Flores Sea.
- C. e. sumbawae* Stresemann, 1925 - Sumbawa, Sumba and Flores (W Lesser Sundas).
- C. e. perneglecta* Mayr, 1944 - Sawu, Alor, Wetar, Kisar, Romang and Damar (E Lesser Sundas).
- C. e. neglecta* G. R. Gray, 1866 - Dao, Roti, Semau and Timor (S Lesser Sundas).
- C. e. amethystina* Salomonsen, 1983 - Waigeo I (off NW New Guinea).
- C. e. erwini* Collin & Hartert, 1927 - W New Guinea, c. 1600 m and above.
- C. e. numforensis* Salomonsen, 1983 - Numfor I (in Geelvink Bay, W New Guinea).
- C. e. nitens* Ogilvie-Grant, 1914 - lowland New Guinea, occasionally to 2500 m, and satellite islands.
- C. e. misimae* Salomonsen, 1983 - Louisiade Archipelago.
- C. e. stresemanni* Rothschild & Hartert, 1914 - Admiralty Is (Manus, Rambutyo, Nauna, Los Negros).
- C. e. kalili* Salomonsen, 1983 - New Hanover, New Ireland and nearby Djaul I (C Bismarck Archipelago).
- C. e. spilogaster* Salomonsen, 1983 - Tabar Is (Tatau) and Lihir Group (NE Bismarck Archipelago).
- C. e. hypogrammica* Salomonsen, 1983 - Green Is including Nissan (E Bismarck Archipelago).
- C. e. tametamele* Stresemann, 1921 - New Britain and nearby Witu Is, and Bougainville I (NW Solomons).
- C. e. becki* Mayr, 1931 - C & NE Solomons (including Malaita).
- C. e. makirensis* Mayr, 1931 - Sañ Cristobal I (SE Solomons).
- C. e. desiderata* Mayr, 1931 - Rennell I (S Solomons).
- C. e. uropygialis* G. R. Gray, 1866 - Santa Cruz Is and Vanuatu (including Torres Is and Banks Is).
- C. e. albidior* Salomonsen, 1983 - Loyalty Is and New Caledonia.



Descriptive notes. 9–10 cm; 8–11 g. Tiny, highly polytypic swiftlet with square tail; generally highly blue-glossed above with brown throat, white belly, mottled flanks and dark undertail. Races *stresemanni*, *natalis*, *tametamele*, *desiderata*, *uropygialis*, *marginata* and *septentrionalis* show varying amounts of white on rump; *manadensis* and *spilura* very dark below, effectively lacking whitish belly; races W of line dividing Philippines, Borneo and Sumatra from Sulawesi and Java have plain rectrices, those E generally have white rectrix spots. Species not capable of echolocation.

Habitat. Appears over a variety of habitats, often associated with human habitation. Prefers humid areas to arid ones. In lowland rainforest zone of Papua New Guinea recorded over forest, forest edge and non-forest. In New Guinea noted from sea-level to 4500 m in Carstenz Massif, more typically to 3600 m, and to 1500 m in Sumatra, though more normally in lowlands. Below 400 m in forest interior on Santa Isabel (Solomon Is). In Wallacea found from sea-level to 1200 m on Sangihe, over 1600 m on Flores, over 1000 m on Sumba and at c. 2000 m on Timor over all habitats.

Food and Feeding. In Malaysia mean foraging heights for preferred forested habitat and open country 52.8 m and 68.0 m respectively; 33% of foraging observed within 10 m of vegetation. Same study revealed following dietary percentages: Hymenoptera 55.2% (Formicoidea 29.6%, Apocrita 2.9%, Meliponidae 13.7%), Diptera 2.1% (Acalypterates 1.3%), Coleoptera 34.0%, Isoptera 1.8% and others 6.9%, with mean prey size 4 mm. At Niah feeds for longer periods on tiny stingless bees (Meliponidae) than sympatric congeners. Often forms large loose flocks. Associates readily with other swiftlets, swifts and hirundines. Forages within forest if aspect open enough. On Sangihe possible niche separation noted, this species often feeding between trees beneath canopy level while *Aerodramus infuscatus* feeds above canopy.

Breeding. Season mainly Feb–Mar Andaman and Nicobar Is. Egg-laying Mar–Aug, peaking Apr, in protracted breeding season, Kuala Lumpur, peninsular Malaysia; also Selangor Feb–Nov, Sumatra Mar and Jun, Flores Mar–Sept, Sumbawa Apr–May, Sumba May, S Sulawesi Nov, Buru Sept, Vanuatu Jun–Feb. Young almost fledged late Sept, Taliabu, Sula Is. Nests in Philippines as follows: Sibuyan Jun, N Luzon and Panay May, Negros May and Sept, and Mindanao Apr–May. In New Guinea breeds apparently in both wet and dry seasons, probably peaking in latter. At Niah, Sarawak, egg-laying occurs in 3 seasons annually: Mar–Apr, mid-Jun to mid-Jul and Oct–Nov, well synchronized both between and within small groups of nests. Nests singly or in colonies, often vast. Nest in New Guinea cup of moss, rootlets, lichens and other vegetable matter attached by saliva to vertical or very steep surface; on Andaman Is shallow, flat-bottomed half-cups 70 mm × 50 mm externally with central depression 20 mm deep, entirely of vegetable matter, attached bracket-like to substrate with brownish saliva. Wide variety of sites including buildings, shallow caves, mouths of large caves, dense overhanging rocks, holes in rocks, hollow trees, among roots of large trees; sometimes dense nest clusters formed; all sites well lit due to lack of echolocation ability; nest-building takes 19–36 days. Two eggs typical, particularly in *cyanoptila*; interval between eggs 2 days; both sexes brood; incubation period 19–24 days, mean 21.5 days. Fledging period varies: where both

On following pages: 16. Linchi Swiftlet (*Collocalia linchi*); 17. Pygmy Swiftlet (*Collocalia troglodytes*); 18. Seychelles Swiftlet (*Aerodramus elaphrus*); 19. Mascarene Swiftlet (*Aerodramus francicus*); 20. Indian Swiftlet (*Aerodramus unicolor*); 21. Philippine Swiftlet (*Aerodramus mearnsi*); 22. Moluccan Swiftlet (*Aerodramus infuscatus*); 23. Mountain Swiftlet (*Aerodramus hirundinaceus*); 24. White-rumped Swiftlet (*Aerodramus spodiopygius*); 25. Australian Swiftlet (*Aerodramus terraereginae*); 26. Himalayan Swiftlet (*Aerodramus brevirostris*).

young survive, 34-50 days, mean 42 days; where both hatch but only 1 survives, 31-46 days, mean 38.5 days; and where only 1 hatches, 28-44 days, mean 36 days; young fed several times daily. Average breeding success 57% with 1-1 young fledged per breeding effort.

Movements. Resident. Australian record as likely to represent undiscovered population as to imply dispersal or vagrancy, though this view not universally supported and there are a number of records from islands in Torres Strait. Recorded only outside breeding season in S Brunei.

Status and Conservation. Not globally threatened. Often abundant, though tends to be scarce or even absent in arid areas of New Guinea. Common in many parts of Sumatra; uncommon in some areas of W New Britain and Solomon Is; common throughout Vanuatu. Malaysian colony at Ampang Reservoir near Kuala Lumpur had c. 10,000 pairs in 1978/79. In Nicobar Is, species is apparently increasing at expense of *Aerodramus fuciphagus*, which is declining as result of overharvesting. Occurs in many protected areas throughout extensive range, e.g. Mount Kinabalu National Park (Borneo) and Gunung-Gede/Pangrango National Park (Java).

Bibliography. Ali & Ripley (1983), Beehler, Pratt & Zimmerman (1986), Beehler, Sengo *et al.* (1995), Blaber (1990), Boles & Barry (1975), Bregulla (1992), Brooks & Dutton (1997), Bryant & Hails (1983), Bryant & Taitner (1990), Cain & Galbraith (1956), Clayton *et al.* (1996), Coates (1985), Coates & Bishop (1997), Cranbrook (1984), Danielsen *et al.* (1994), Davison (1992, 1997a), Delacour & Mayr (1945), Dickinson (1989b), Dickinson *et al.* (1991), Evans, Dutton & Brooks (1993), Evans, Magsalay *et al.* (1993), Finch & McKean (1987), Gibson-Hill (1947), Giliardi (1950a), Giliardi & LeCroy (1961), Goodman & Gonzales (1990), Grimmett *et al.* (1998), Hachisuka (1930, 1934), Hails & Amirudin (1981), Hails & Turner (1985), Hannecart & Létocart (1980), Harrison (1974), Hicks (1992a), Higgins (1999), Holmes & Philipps (1996), Inskipp *et al.* (1996), Isherwood *et al.* (1997), Jepson (1997), Lambert (1994), LeCroy & Peckover (1983), Lee *et al.* (1996), Lekagul & Round (1991), Lim Kim Seng (1992), Mackay (1968), MacKinnon & Philipps (1993), Madoc (1976), Manuel (1937, 1939), van Marle & Voous (1988), Mayr (1931, 1944, 1945), Mayr & Rand (1937), McGregor (1904, 1905, 1907a, 1907b, 1910), McKean (1967), McNab & Bonaccorso (1995), Medway (1962a, 1962b, 1966), Medway & Pye (1977), Medway & Wells (1976), Mees (1965), Meyer de Schauensee & Ripley (1940), Novick (1959), Oberholser (1906), Parkes (1960b), Parrott & Andrew (1996), Peters (1939), Rabor (1952, 1954, 1955, 1977), Rand & Giliardi (1967), Rand & Rabor (1960), Riley, J. (1997a), Riley, J.H. (1938), Ripley (1964a), Ripley & Rabor (1958), Rothschild & Hartert (1914), Salomonsen (1983), Schodde (1977), Smythies (1981, 1986), Somadikarta (1982, 1986), Spennemann (1928), Stokes (1988), Strahan (1994), Stresemann (1912, 1925), Stresemann & Paludan (1932), Tikader (1984), Waugh & Hails (1983), Webb (1992, 1997), Wells (1999), White & Bruce (1986).

16. Linchi Swiftlet

Collocalia linchi

French: Salangane linchi **German:** Linchisalangane **Spanish:** Salangana Linchi
Other common names: Cave Swiftlet

Taxonomy. *Collocalia linchi* Horsfield and F. Moore, 1854, Java.

May be conspecific with *C. esculenta*; some authors place race *C. e. natalis* in present species. Older synonym for species, *C. fucivora* (Streubel, 1848), is a forgotten name. Four subspecies recognized.

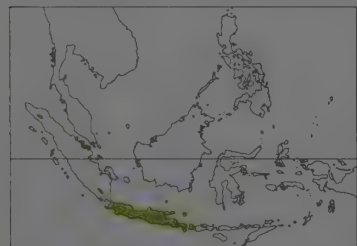
Subspecies and Distribution.

C. l. ripleyi Somadikarta, 1986 - N & S Bukit Barisan, Sumatra.

C. l. dodgei Richmond, 1905 - Mt Kinabalu (Sabah).

C. l. linchi Horsfield & F. Moore, 1854 - Madura, Bawean and Nusa Penida Is and Java.

C. l. dedii Somadikarta, 1986 - Bali and Lombok.



Descriptive notes. 10 cm. A tiny swiftlet with a square tail; plumage very similar to that of *C. esculenta* but green-glossed and lacks rectrix spots; in the hand, differs from *C. esculenta* by absence of feather tuft on hind toe, though this feature and perhaps even plumage gloss seem equivocal. Race *dodgei* has shorter wings and tail; *ripleyi* considerably shorter tail and more pronounced dark shafts to abdomen feathers; *dedii* longer wings and tail, with darker plumage. Species not capable of echolocation.

Habitat. Occurs from sea-level up into highlands, over both forest and open country. In Sumatra and Borneo, occurs only at high altitude. On Lombok recorded from sea-level up to over 500 m.

Food and Feeding. Gregarious. Will forage in crowns of emergent trees, particularly fruiting figs.

Breeding. Self-supporting bracket-shaped nest consisting of thin pieces of vegetable matter, species used depending on availability. Two white elongate eggs.

Movements. Resident.

Status and Conservation. Not globally threatened. Believed to be extinct on Malay Peninsula. Apparently rarest in Sumatra. Race *dodgei* seen in good numbers on Mt Kinabalu in 1988. Common on Java and satellite islands. Practice reported from Java of converting house-based colonies of this species into colonies of *Aerodramus fuciphagus* to profit from edible-nest harvest will reduce number of colonies.

Bibliography. Andrew (1985), Clayton *et al.* (1996), Coates & Bishop (1997), Duckworth & Kelsh (1988), Hellebrekers & Hoogerwerf (1967), Inskipp *et al.* (1996), Junge (1936), Lee *et al.* (1996), MacKinnon (1988), MacKinnon & Philipps (1993), van Marle & Voous (1988), Mason (1989), Medway (1962d, 1966), Medway & Pye (1977), Meyer de Schauensee & Ripley (1940), Peters (1940b), Richmond (1905), Salomonsen (1983), Smythies (1981), Somadikarta (1982, 1986), Spennemann (1928), White & Bruce (1986).

17. Pygmy Swiftlet

Collocalia troglodytes

French: Salangane pygmée **German:** Zwergsalangane **Spanish:** Salangana Chica

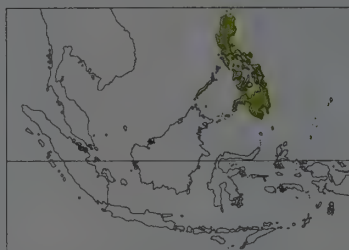
Taxonomy. *Collocalia* [sic] *troglodytes* G. R. Gray and Mitchell, 1845, Philippines. Monotypic.

Distribution. Philippines including Palawan, but not Sulu Archipelago.

Descriptive notes. 9 cm. Tiny swiftlet with square tail; black upperparts with neat, well-defined white rump band; mottled underparts with brown throat, whitish belly and dark undertail-coverts. From Philippine races *marginata* and *septentrionalis* of *C. esculenta* by pure white, not mottled, grey-white band. Uncertain whether or not species is capable of echolocation.

Habitat. A lowland species, most frequently encountered over forest and inland water.

Food and Feeding. Typically forages in small groups.



Breeding. Season on Mindanao, May and Jul; on Bohol, Apr; Negros, Apr; Luzon, young in nest in Sept. Half-cupped, self-supporting, bracket-shaped nest of vegetable matter bound with hard, white, translucent saliva; edibility uncertain.

Movements. Resident.

Status and Conservation. Not globally threatened. Fairly common to common. Recently recorded as common in Rajah Sikatuna National Park, Bohol. Commonly represented in collections of swiftlets taken from Philippines over many decades.

Bibliography. Brooks, Dutton *et al.* (1996), Brooks, Magsalay *et al.* (1995), Danielsen *et al.* (1994), Delacour & Mayr (1946), Dickinson (1989b), Dickinson, Kennedy & Parkes (1991), Dickinson, Kennedy, Read & Rozendaal (1989), Evans, Dutton & Brooks (1993), Gogorza y González (1987), Kutter (1982), Lee *et al.* (1996), Manuel (1937), McGregor (1903, 1906, 1907b, 1909), Medway (1966), Medway & Pye (1977), Meyer de Schauensee & duPont (1962), Oberholser (1906), duPont (1971), duPont & Rabor (1973b), Rabor (1938b, 1954, 1977), Rand & Rabor (1960), Salomonsen (1983).

Genus AERODRAMUS^o Oberholser, 1906

18. Seychelles Swiftlet

Aerodramus elaphrus

French: Salangane des Seychelles **German:** Seychellensalangane **Spanish:** Salangana de Seychelles
Other common names: Seychelles Cave Swiftlet

Taxonomy. *Collocalia fuciphaga elaphra* Oberholser, 1906, Mahé Island, Seychelles.

Genus often merged into *Collocalia*. Forms superspecies with *A. francicus*, and sometimes considered conspecific. Monotypic.

Distribution. La Digue, Mahé and Praslin, Seychelles. Formerly occurred on Felicite.



Descriptive notes. 11 cm; 10.5 g. Small swiftlet with forked tail; brown upperparts with rump marginally paler, underparts paler mid-brown. In hand has copious white rami of back feathers, and longer wings and larger bill than *A. francicus*. Available information suggests species probably capable of echolocation.

Habitat. Occurs over wide variety of habitats, including forest and wetlands, from lowlands up into highlands.

Food and Feeding. Flying ants predominated in a study of food brought in to young. Species is gregarious, foraging over various types of habitat.

Breeding. May breed throughout year, and certainly extended as colonies visited early Jul 1970 contained eggs and young of various ages; season initially thought to relate to SE monsoon from Jun to Nov. Nests in caves, at 1 site created by a number of huge granite boulders in a valley where 2 colonies of 14 and 23 nests in 1970. Bracket-shaped, self-supporting nest of grey-green lichen strands agglutinated with saliva, strong, yet dry and flexible; nest hinge dark brown with large quantity of saliva; nest 55 mm high × 105 mm wide, with depression 35 mm front to back. One egg typical. Replacement clutches and fresh clutches after successful fledging within 14 days; incubation period 25-30 days; fledging period 42 days.

Movements. Resident. Recorded as a wanderer to Aride.

Status and Conservation. VULNERABLE. Restricted-range species; present in Granitic Seychelles EBA. Lack of additional suitable sites may limit both population and distribution. Disturbance and vandalism have caused concern, and fitting of metal grilles across cave entrances has been recommended. Vulnerable also to alien predators, especially cats and Common Barn-owls (*Tyto alba*). Recent increase on La Digue may be due to changed hydrological conditions or immigration from former colony on Felicite. Overall population believed to number 2500-3000 birds. Mahé population estimated at 2263 (±371) individuals using capture-recapture technique in Mar 1997, while La Gogue colony estimated at 500-600 nests in Jan 1996. It is likely, especially in Morne Seychelles National Park, that undiscovered cave colonies exist. Only known Praslin population is Mt Cabris colony where there were 79 nests in Apr 1997; cave of colony at L'Amitié has been destroyed, and colony believed to be at Fond d'Azore cannot be located. Two colonies above La Réunion had 35-45 nests in 1997.

Bibliography. Benson (1967b), Bullock (1990), Clayton *et al.* (1996), Collar & Andrew (1988), Collar & Stuart (1985), Collar *et al.* (1994), Diamond & Fearn (1980), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Evans (1977), Gaymer *et al.* (1969), Gerlach (1997), Lee *et al.* (1996), Loustau-Lalanne (1962), MacDonald (1978), Medway (1966), Mountfort (1988), Newton (1867), Oberholser (1906), Penny (1974), Pratt (1986), Procter (1970, 1972), Rocamora (1997), Rocamora & Skerrett (1999), Sinclair & Langrand (1998), Stattersfield *et al.* (1998), Vesey-Fitzgerald (1936), Watson, G.E. *et al.* (1963), Watson, J. (1979, 1984).

19. Mascarene Swiftlet

Aerodramus francicus

French: Salangane des Mascareignes **German:** Mauritius-salangane **Spanish:** Salangana de las Mascareñas
Other common names: Grey-rumped(!) Indian Ocean/Mascarene Cave/Mauritius Swiftlet

Taxonomy. *Hirundo francica* J. F. Gmelin, 1789, Mauritius.

Genus often merged into *Collocalia*. Forms superspecies with *A. elaphrus*, and sometimes considered conspecific; has alternatively been lumped with *A. fuciphagus*, although the two do not appear to be closely related. In past, was treated as part of a composite species also including *A. infuscatus*,

A. hirundinaceus, *A. spodiopygius* and *A. terraereginae*. Differences between birds on Reunion and Mauritius suggest that two subspecies may be involved. Monotypic.

Distribution. Mauritius and Reunion (Mascarenes).



Descriptive notes. 10.5 cm; 9.9-5 g. Small swiftlet with forked tail; dark brown upperparts with whitish rump clearly paler, pale brown underparts. Species capable of echolocation.

Habitat. Occurs over wide range of habitats. Nesting caves are typically sited in lava tunnels.

Food and Feeding. Gregarious, foraging in flocks. Usually feeds at least 20 m above ground, though will feed lower over lakes and during cloudy periods. In 2 boluses of prey collected by adults to feed nestlings. Diptera predominated; most prey 1.6-3.2 mm long, though some flying ants 5.2-8.2 mm with an

anthomyid fly measuring 4-2 mm. Foraging ends never more than 35 minutes after dark and more typically within 30 minutes.

Breeding. Season not clearly defined with eggs and young present in every month except Apr and May 1974 in a 16-month study of 2 colonies from Oct 1973 to Jan 1975, and even during these months nests were being built; these 2 sites, though close, were not in synchrony. Openings of subterranean waterways typically used for breeding, often sited in canefields. Self-supporting, bracket-shaped nest of lichen filaments agglutinated with saliva which is copious only in hinge; mean 62.5 mm x 55 mm and 30 mm deep. Two eggs typical, 1 rarely; 4 weeks from starting fresh nest to laying, or 4-6 weeks if nest destroyed, though slower if starting again after a non-breeding period; mean relaying interval 27 days; interval between clutches c. 3 weeks, allowing for 2 broods in 6-5 months or 3 in 9-5 months. Incubation period probably 21-23 days; mean fledging period probably 45-55 days. Hatching success high, 84% in non-vandalized nests, but 24 of 44 nests destroyed by vandals.

Movements. Resident. Records from Madagascar no longer considered acceptable.

Status and Conservation. Not globally threatened. Currently considered near-threatened. Restricted-range species: present in Reunion EBA and Mauritius EBA. Population limited by paucity of suitable nest-sites. Generally rather common to locally abundant on Reunion and Mauritius. On Reunion several colonies threatened by actions of speleologists, while many cave sites inaccessible which, though granting protection, limits estimation of population size.

Bibliography. Barré (1983, 1988), Barré *et al.* (1996), Berlioz (1946), Cheke (1987b, 1987c), Cheke & Jones (1987), Clayton *et al.* (1996), Collar *et al.* (1994), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Gill (1971), Horne (1987), Langrand (1995), Langrand & Sinclair (1994), Lee *et al.* (1996), Mayr (1937a), Medway (1966), Medway & Pye (1977), Michel (1992), Milon (1951), Oberholser (1906), Pratt (1986), Procter (1972), Rand (1936), Rountree *et al.* (1952), Sargeant (1992b), Sims (1961), Sinclair & Langrand (1998), Stattersfield *et al.* (1998), Staub (1973, 1976), Stresemann (1925).

20. Indian Swiftlet

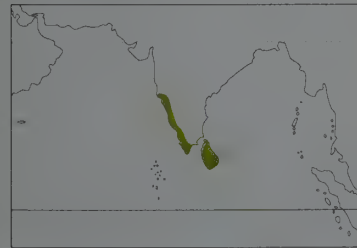
Aerodramus unicolor

French: Salangane de Malabar **German:** Malabarsalangane **Spanish:** Salangana de Malabar
Other common names: Indian Edible-nest Swiftlet(!)/Swift

Taxonomy. *Hirundo unicolor* Jerdon, 1840, Coonoor Pass.

Genus often merged into *Collocalia*. Previously considered conspecific at various times with *A. brevirostris* or *A. fuciphagus*; has also been associated with *A. francicus* and *A. elaphrus*, due mainly to relative geographical proximity; probably closest to *A. vanikorensis* group. *A. brevirostris rogersi* has been tentatively linked with present species on morphological grounds. Monotypic.

Distribution. SW India, from S Maharashtra S through Western Ghats to Kerala and W Tamil Nadu, and throughout Sri Lanka.



Descriptive notes. 12 cm. Medium-sized swiftlet with shallow tail-fork; dark brown upperparts with uniform or marginally paler rump; uniformly pale brown underparts and unfeathered tarsi. In hand from *A. brevirostris* by smaller size (very little overlap), less glossy and slightly paler upperparts. Species capable of echolocation.

Habitat. From lowlands, wherever there are rocky hills with suitable nesting caves, to 2200 m over a variety of habitats, though on Sri Lanka primarily an upland species. Occurs over scrub and dry deciduous forest at Mudumalai Wildlife Sanctuary, India. Fre-

quents small rocky offshore islands as well as mainland habitats.

Food and Feeding. Diptera, Hemiptera and Hymenoptera predominate with Coleoptera, Odonata and Trichoptera also recorded. Two jassid mango-hoppers, *Ideocerus niveosparus* and *I. atkinsoni*, presumably taken over nearby mango orchards, accounted for 80% of 4 stomach contents examined. On Sri Lanka recorded taking prey from around lights at night; nestlings were fed well into night.

Breeding. Season mainly Mar-Jun, S India; nest-building late Dec to early Jan with second brood, if harvesting has not occurred, in Aug-Sept, Sri Lanka. Nests colonially in caves, including sea-caves, railway tunnels, etc. Self-supporting, bracket-shaped nest, 65-80 mm wide x 20-25 mm deep, with sparse to moderate plant content and often feathers, agglutinated with firm, whitish saliva; hinge and some whole nests made almost entirely of saliva, imparting "edible" qualities; nests often infested with bed bugs (*Cimex rotundatus*); large numbers of nests often densely clustered. Two eggs; double-brooded Sri Lanka; young cling to outside of nest when half-grown.

Movements. Believed resident, though probably occasional winter visitor to Maldives.

Status and Conservation. Not globally threatened. Particularly abundant in Sri Lanka, where is one of most abundant of mountain bird species; also abundant in cave systems of Western Ghats, and on islands off Malabar coast. Colony at Venguria, Western Ghats, in 1940's contained c. 5000 birds. Present in several protected areas, e.g. Mudumalai National Park (SW India) and Ingiriya Forest Reserve (Sri Lanka). In Sri Lanka illegal nest harvesting has resumed since 1993, with collection noted in Central, Uva and Sabaragamuwa Provinces, despite protection by law; although short time since resumption of this activity makes assessment of population trends difficult, it has

been noted that no young have fledged in surveyed caves from which collection has taken place and that some caves appear to have been abandoned completely.

Bibliography. Abdullali (1942), Aitken (1895), Ali (1996), Ali & Ripley (1983), Chakravarthy & Purna Chandra Tejasvi (1992), Daniels (1997), Foulkes (1904), Gokula & Vijayan (1997), Grewal (1995), Grimmett *et al.* (1998), Gunawardana (1997), Henry (1998), Inskipp *et al.* (1996), Kannan (1998), Lamsfuss (1998), Medway (1966), Medway & Pye (1977), Novick (1959), Oates (1890), Oberholser (1906), Phillips (1963, 1978), Pratt (1986), Procter (1972), Ripley (1964b, 1982), Whistler (1936).

21. Philippine Swiftlet

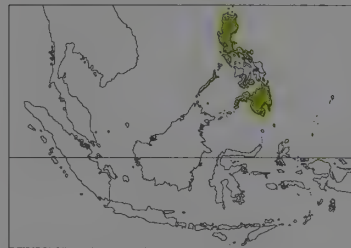
Aerodramus mearnsi

French: Salangane de Mearns **German:** Braunbüzelsalangane **Spanish:** Salangana Filipina
Other common names: Philippine Grey Swiftlet, Brown-rumped Swiftlet(!)

Taxonomy. *Collocalia fuciphaga mearnsi* Oberholser, 1912, Hights in the Oaks, near Pauai, Benguet, Luzon.

Genus often merged into *Collocalia*. Forms superspecies with *A. infuscatus*, *A. hirundinaceus*, *A. spodiopygius* and *A. terraereginae*. Previously placed in the *A. vanikorensis* superspecies. Monotypic.

Distribution. Philippines, on Luzon, Mindoro, Palawan, Negros, Bohol and Mindanao.



Descriptive notes. 10-10.5 cm. Small swiftlet with shallow tail-fork; dark brown upperparts with uniform rump; paler mid-brown underparts. In hand from slightly smaller, sympatric *A. vanikorensis amelis* by tarsus feathering, smaller, more decurved bill, less forked tail, and white tips to rami of rump feathers. No information available as to whether or not species is capable of echolocation.

Habitat. Primarily a submontane species. Recorded breeding at 1600 m on Mt Halcon, Mindoro, and at 700 m on Bohol.

Food and Feeding. Unknown, but should resemble that of other *spodiopygius* group members.

Breeding. Nests originally thought to belong to *A. vanikorensis amelis* 700 m inside Miatan Caves, Mindanao, in May 1952 were shallow saucers placed in rock cavities and are now believed to have been nests of *A. mearnsi*. Nests consist of moss held together with saliva which does not remain moist but hardens. Breeds May on Mindoro. Four eggs.

Movements. Resident.

Status and Conservation. Not globally threatened. Uncommon. Recently recorded as rare in Rajah Sikatuna National Park, Bohol; also present in Mount Canlaon National Park (Negros) and Mount Katanglad National Park (Mindanao). Problems of identification render estimations of true status difficult; however, scarcity of museum specimens suggests that species may well be genuinely uncommon.

Bibliography. Brooks & Dutton (1997), Brooks, Dutton *et al.* (1996), Brooks, Evans *et al.* (1992), Brooks, Magsalayan *et al.* (1995), Danielsen *et al.* (1994), Dickinson (1989a), Dickinson *et al.* (1991), Dutton *et al.* (1992), Evans, Dutton & Brooks (1993), Gilliard (1950a), Inskipp *et al.* (1996), Oberholser (1912), duPont (1971), Ripley & Rahor (1958).

22. Moluccan Swiftlet

Aerodramus infuscatus

French: Salangane des Moluques **German:** Molukksalangane **Spanish:** Salangana Moluqueña

Taxonomy. *Collocalia infuscata* Salvadori, 1880, Ternate.

Genus often merged into *Collocalia*. Forms superspecies with *A. mearnsi*, *A. hirundinaceus*, *A. spodiopygius* and *A. terraereginae*. Previously placed in composite species *A. francicus* or alternatively in *A. vanikorensis*; considered conspecific with *A. spodiopygius* by some authors. Three subspecies recognized.

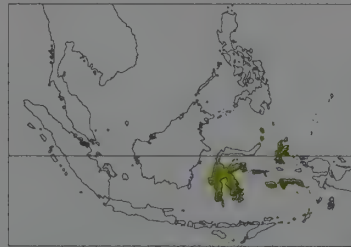
Subspecies and Distribution.

A. i. sororum (Stresemann, 1931) - Sulawesi.

A. i. infuscatus (Salvadori, 1880) - N Moluccas (Ternate, Halmahera and Morotai, and possibly Bacan and Obi), and recently recorded on Sangihe and Siau.

A. i. ceramensis (van Oort, 1911) - S Moluccas (Buru, Boano, Ambon and Seram).

Recently recorded in Sula Is (Taliabu), but racial identity unknown.



Descriptive notes. 10 cm. Small swiftlet with forked tail and broad wings with slightly bulging secondaries; upperparts black-brown with rump uniform or slightly paler and greyish; underparts pale brown. Race *sorum* has broader, distinct, grey-white rump band, 6-7 mm, and silvery grey underparts with brownish throat; *ceramensis* has broadest and whitest rump band, 10-12 mm. Differs from sympatric races of *A. vanikorensis*, notably *waigeuensis*, by greater tendency towards tarsal feathering (care required, as equivocal), paler underparts and extensively white rami on rump feathers. No information available as

to whether or not species is capable of echolocation.

Habitat. Generally appears to occur at higher altitude than closest sympatric congener, though collected on Sulawesi at 50-2500 m, on Seram at c. 700 m, on Sangihe from sea-level to 1200 m, and on Buru to 750 m.

Food and Feeding. On Sangihe possible niche separation noted, this species often feeding above canopy while *Collocalia esculenta* fed between trees beneath canopy level.

Breeding. Thought to make a nest consisting of vegetable matter and attached to cave wall.

Movements. Resident. May be nomadic.

Status and Conservation. Not globally threatened. Not uncommon on Seram at 700 m; common on Sangihe, though less so at lower altitudes, and especially common at higher altitudes on Gunung Awu. Present in Dumoga-Bone and Lore Lindu National Parks (Sulawesi) and Manusela National Park (Seram).

Bibliography. Bowler & Taylor (1989), Browning (1993), Coates & Bishop (1997), Inskipp *et al.* (1996), Isherwood *et al.* (1997), Jepson (1993), Lambert (1994), Mayr (1937a), Pratt (1986), Riley (1997a), Rozendaal & Dekker (1989), Salomonsen (1983), Stones, Lucking *et al.* (1997), Stresemann (1914a, 1932, 1940), Wardill (1995), Watling (1983), White & Bruce (1986).

23. Mountain Swiftlet

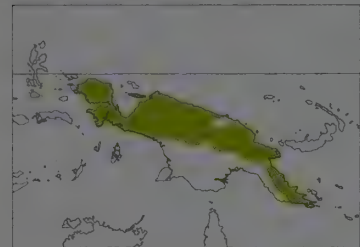
Aerodramus hirundinaceus

French: Salangane de montagne German: Bergsalangane Spanish: Salangana Montana

Taxonomy. *Collocalia fuciphaga hirundinacea* Stresemann, 1914, Upper Utakwa River, New Guinea. Genus often merged into *Collocalia*. Forms superspecies with *A. mearnsi*, *A. infuscatus*, *A. spodiopygius* and *A. terraereginae*. Previously placed in composite species *A. francicus* or alternatively in *A. vanikorensis*; considered conspecific with *A. spodiopygius* by some authors. Three subspecies recognized.

Subspecies and Distribution.

A. h. baru (Stresemann & Paludan, 1932) - Yapen I (in Geelvink Bay, NW New Guinea).
A. h. excelsus (Ogilvie-Grant, 1914) - over 1600 m in Snow Mts and Carstenz peaks, Irian Jaya.
A. h. hirundinaceus (Stresemann, 1914) - much of New Guinea.



Descriptive notes. 11-13 cm. A medium-sized swiftlet with a moderately forked tail; uniform dark brown upperparts, some birds with a suggestion of a paler rump; underparts pale grey to mid-grey, though mid-throat can be dark. Differs from sympatric *A. vanikorensis* by feathered tarsi, tiny, more decurved bill, greater white in rami of back, darker, more blue-glossed upperparts and clearly paler underparts. Race *baru* has very dark upperparts, browner underparts and heavy tarsal feathering; *excelsus* much larger than nominate. Species capable of echolocation.

Habitat. Occurs over wide range of habitats, mainly in highlands, where recorded to 4000 m. Relatively low numbers can be encountered in lowlands where there are adjacent hills.

Food and Feeding. Gregarious, commonly foraging in association with other swifts.

Breeding. Active colony noted late Sept. Tari District, Southern Highlands Province; birds entering possible nest-site in Jun on Karkar I. Colonial breeder. Externally supported nest is bulky structure of mosses, filmy ferns, grasses and rootlets bound to central core, sited in dimly lit or completely dark situations; in some high-altitude breeding caves nests can be sited on floor, presumably because their main predators there, snakes, are infrequent above 1000 m. Little or no saliva used for agglutination or attachment to narrow rock ledge or niche. One egg.

Movements. Nomadic movements may account for occasional absence of the species from some parts of range.

Status and Conservation. Not globally threatened. Generally scarce in lowlands, locally common to abundant in highlands. Commonly represented in collections of swiftlets from New Guinea over many decades.

Bibliography. Beechler (1978), Beechler *et al.* (1986), Bravery (1972), Clapp (1986, 1987), Clayton *et al.* (1996), Coates (1985), Diamond (1972), Fenton (1975), Gilliard & LeCroy (1961), Gregory (1995a, 1995b), Hadden (1975), Mackay (1991), Mayr (1937a), Mayr & Rand (1937), Medway (1966), Medway & Pye (1977), Murray (1988), Pratt (1986), Rand (1942a), Rand & Gilliard (1967), Ripley (1964a), Salomonsen (1983), Schodde & McKean (1972), Stresemann & Paludan (1932), Tarburton (1990b).

24. White-rumped Swiftlet

Aerodramus spodiopygius

French: Salangane à croupion blanc German: Weißbürtzelsalangane Spanish: Salangana Culiblanca

Other common names: Grey(!)/Grey-rumped(!) Swiftlet, Pacific White-rumped Swiftlet

Taxonomy. *Macropteryx spodiopygius* Peale, 1848, Upolu and Tutuila, Samoa Islands.

Genus often merged into *Collocalia*. Forms superspecies with *A. mearnsi*, *A. infuscatus*, *A. hirundinaceus* and *A. terraereginae*, and last three have all been considered conspecific with present species. *A. sawiellii* may prove to be merely a race of present species. Previously placed in composite species *A. francicus*. Eleven subspecies recognized.

Subspecies and Distribution.

A. s. delichon (Salomonsen, 1983) - Admiralty Is.
A. s. eichhorni (Hartert, 1924) - Mussau I in St Matthias Group (NC Bismarck Archipelago).
A. s. noonaedanae (Salomonsen, 1983) - New Ireland and New Britain.
A. s. reichenowi (Stresemann, 1912) - S & E Solomon Is.
A. s. desolatus (Salomonsen, 1983) - Duff Is, Swallow Is and Santa Cruz Is.
A. s. epiensis (Salomonsen, 1983) - N & C Vanuatu.
A. s. ingens (Salomonsen, 1983) - S Vanuatu.
A. s. leucopygius (Wallace, 1864) - Loyalty Is and New Caledonia.
A. s. assimilis (Stresemann, 1912) - Fiji.
A. s. townsendi (Oberholser, 1906) - Tonga.
A. s. spodiopygius (Peale, 1848) - Samoa.



Descriptive notes. 10-11.5 cm; one female 8 g. A small to medium-sized swiftlet with a deep tail-fork; highly polytypic. Rump pale throughout, but degree of paleness varies geographically. Most races are much paler below than *A. vanikorensis*, practically pure white in the case of *leucopygius*, although throat is often rather dark; races *townsendi*, *desolatus* and *epiensis* are sooty below. Degree of tarsal feathering is variable both within and especially among races; heavily feathered in *epiensis* and *ingens*, though unfeathered or only lightly feathered in most other races; in *ingens*, dark brown face shows greater contrast with pale underparts. Species capable of echolocation.

Habitat. Occurs over wide range of island habitats, from lowlands to highlands, on New Britain to 1890 m and on Bougainville to 1600 m. On Santa Isabel occurs above 700 m over montane forest.

Food and Feeding. Race *assimilis* of Fiji compared with *A. terraereginae chillagoensis* of Australia: present species takes smaller prey in smaller boluses, containing more individuals; 32 boluses

of present species contained 167 species of invertebrate, whereas 32 boluses of *A. terraereginae* contained 303 species, averaging 10 species more per bolus than in present species. Can be encountered foraging in large groups, alone or with sympatric congeners. Forages over a range of elevations.

Breeding. Season on Vanuatu Oct-Feb; active colony reported on Lou I (S of Manus in Admiralty Is), Mar; on Fiji first eggs laid Sept-Oct, most chicks fledging Jan, but replacement clutches extend season into Feb, sometimes Mar. Colonial. Nests in caves, including sea-caves, or similar situations, including man-made structures, but also below overhanging rocks in gulleys or under fallen trees; mainland sites are used, as well as island ones. Substantial self-supporting, bracket-shaped nest with shallow central depression, consisting of fine vegetable matter; on Fiji lichens, liverworts, filmy ferns and mosses predominate, though grasses used extensively at 1 site, agglutinated with firm saliva and attached to cave walls; nests sometimes cylinder-shaped where birds add to them each time they breed. On Fiji nests of *assimilis* typically closely bunched, though sometimes 1-2 m apart and exceptionally 70 m, often attached not to wall but to other nests; measure 50 × 50 × 21 mm, mean volume index 52.5 cm³. Clutch of 1 or 2 white eggs, though mean of 57 clutches 1-98; laying interval 3-5 days, mean 4; incubation period 22-25 days, shared by both parents who also brood at night; lost clutches and even lost broods typically replaced within 9-14 days; evidence suggests that sometimes more than 1 female lays eggs in same nest. Second chick hatches within 1-5 days of first; nestling period 45-46 days; daily feeding rate 2-8 visits. Average breeding success 53%, with 1-1 young fledged per breeding effort.

Movements. Resident. Vagrant to New Zealand.

Status and Conservation. Not globally threatened. Fairly common to abundant over much of range; 8 colonies in Fiji contained over 1400 nests in 1975 and 1976. Commonest swiftlet in W New Britain. However, decline noted in some parts of range, e.g. by 1960's *epiensis* occurred, uncommonly, only on Malo I and W coastal Espiritu Santo I in Vanuatu. Local and uncommon on Santa Isabel, Solomon Is.

Bibliography. Banks (1984), Bregulla (1992), Cain & Galbraith (1956), Clayton *et al.* (1996), Clunie (1984), Coates (1985), Engbring & Ramsey (1989), Finch & McKean (1987), Hadden (1981), Hannecart & Léocart (1980), Hicks (1992a), Holyoak (1979), LeCroy & Peckover (1983), Lee *et al.* (1996), Mayr (1945), Medway (1966), Medway & Pye (1977), Muse & Muse (1982), Pratt (1986), Pratt *et al.* (1987), Reed (1980), Rinke (1987), Salomonsen (1983), Stresemann (1912, 1926), Stresemann & Paludan (1932), Suthers & Hector (1982), Tarburton (1986a, 1986b, 1986c, 1987a, 1987b, 1988a, 1988b, 1990b, 1993a, 1993b), Tarburton & Minot (1987), Vuilleumier & Gochfeld (1976), Watling (1982), Webb (1992).

25. Australian Swiftlet

Aerodramus terraereginae

French: Salangane d'Australie German: Queenslandsalangane Spanish: Salangana Australiana Other common names: Grey Swiftlet(!)

Taxonomy. *Cypselus terra-reginae* E. P. Ramsay, 1875, north-east coast ranges, near Cardwell, Queensland.

Genus often merged into *Collocalia*. Forms superspecies with *A. mearnsi*, *A. infuscatus*, *A. hirundinaceus* and *A. spodiopygius*. Previously placed in composite species *A. francicus* or alternatively in *A. vanikorensis*; considered conspecific with *A. spodiopygius* by some authors. Race *chillagoensis* has even been treated as a separate species, although solid grounds for such a split would appear to be lacking. Two subspecies recognized.

Subspecies and Distribution.

A. t. terraereginae (E. P. Ramsay, 1875) - coastal N Queensland.
A. t. chillagoensis Pecotich, 1982 - Chillagoe, Mitchell and Palmer districts, inland Queensland.



Descriptive notes. 11 cm; 9.5 g. Medium-sized swiftlet with shallowly forked tail; dark brown upperparts with typically paler rump; though some birds uniform across upperparts; pale grey-brown underparts; tarsi heavily feathered and tail proportionally long for *A. spodiopygius* group. Race *chillagoensis* is smaller and paler. Species capable of echolocation.

Habitat. Recorded to 1000 m, generally below 500 m. Much foraging over dry savanna-type terrain, though also seen feeding at rainforest margin. Breeds in both island and mainland sites.

Food and Feeding. Habits of race *chillagoensis* compared with those of *A. spodiopygius assimilis* of Fiji: present species takes larger prey in larger boluses, containing fewer individuals; 32 boluses contained 303 invertebrate species, averaging 10 species more per bolus than in *A. spodiopygius*; 32 boluses of latter contained only 167 species. Large numbers of present species leave nest cave at regular intervals during day to feed locally; after c. 30 minutes they return to cave for 10 minutes of lesser activity. Feeds less than 30 km from breeding sites.

Breeding. At Tully Gorge, North Queensland, 95% of nests contained eggs or nestlings at various stages of development, early Oct to mid-Jan; breeds at Chillagoe, Oct-Mar. Colonial, averaging 77 nests Chillagoe. Nesting caves totally dark or with little twilight; nests 2-20 m above cave floor on smoothly concave walls, though extrusions or cracks readily utilized; at 1 large colony average distance between nests 8 cm. At Chillagoe kangaroo grass (*Themeda australis*) and black spear grass (*Heteropogon contortus*) commonest nesting materials; 1 nest made of *Casuarina* twigs agglutinated with laminae of firm translucent saliva. Shallower nests than those of *A. spodiopygius*: nest of nominate race 56 × 45.5 × 3 mm, mean volume index 7.5 cm³; *chillagoensis* 49 × 42.5 × 12 mm, mean 25 cm³. One egg, laying apparently stimulated by rain; mean incubation 26.5 days, both sexes incubating; lost clutches and broods less than 10 days old replaced within 6-18 days. Nestling period 46 days in good season, 51 in poor season. Second clutch also of 1 egg laid 50 days after first, uses heat from first nestling to aid incubation. Feeding rates 5 per day in good season, 2 per day in bad season.

Movements. Resident.

Status and Conservation. Not globally threatened. Common in lowlands. Survey of 34 active colonies during 1985-1987 showed peak count of 500 pairs for a single colony. Range appears stable but diminished numbers of breeding birds recorded at several colonies. It has been suggested that frequency of sightings away from areas with colonies implies new colonies will be found.

Bibliography. Blakers *et al.* (1984), Busst (1956), Cassels (1961), Clayton *et al.* (1996), Coles *et al.* (1987), Crouther (1983a, 1983b), Griffin (1969), Higgins (1999), Lee *et al.* (1996), Lindsey (1992), Macdonald (1988), Medway (1966), Medway & Pye (1977), Pecotich (1974), Pecotich & Collins (1966), Pizzey & Doyle (1998), Pratt (1986), Salomonsen (1983), Schodde & Tidemann (1986), Schulz (1991), Seton (1965), Simpson & Day (1998),

Smyth (1976, 1980), Smyth *et al.* (1980), Storr (1984), Strahan (1994), Stresemann & Paludan (1932), Tarburton (1988a, 1988b, 1993b), Tarburton & Minot (1987), Trounson & Trounson (1987), Wheeler (1959).

26. Himalayan Swiftlet

Aerodramus brevirostris

French: Salangane de l'Himalaya

German: Himalayasalangane

Spanish: Salangana del Himalaya

Other common names: (Indian) Edible-nest Swiftlet(!), Himalayan Swift; Chinese Swiftlet (*innominatus*); Indochinese Swiftlet (*rogersi*); Volcano Swiftlet (*vulcanorum*)

Taxonomy. *Hirundo brevirostris* Horsfield, 1840, Assam.

Genus often merged into *Collocalia*. Races *vulcanorum* and *rogersi* may represent distinct species, particularly the former; *rogersi* may be closely related to *A. unicolor*, but intergrades between *rogersi* and other races of present species may occur; *vulcanorum* has alternatively been considered a race of *A. maximus*. Formerly linked with *A. whiteheadi*, but differs in nest type and rump pattern. Proposed races *inopinus* and *capnitis*, both from Hubei (EC China), are synonyms of *innominatus*; rump colour varies within populations of *innominatus*, dark-rumped individuals having been described as race *pellios*. Four subspecies currently recognized.

Subspecies and Distribution.

A. b. brevirostris (Horsfield, 1840) - Himalayas and mountains of NE India, SC China (W Yunnan), Myanmar and Thailand; winters to SW Thailand and Malay Peninsula and possibly Sumatra.

A. b. innominatus (Hume, 1873) - EC & SC China (Hubei, S Sichuan, N Guizhou, Yunnan) and N Vietnam (NW Tonkin); winters to SW Thailand and Malay Peninsula, occasionally to Andaman Is and possibly Sumatra.

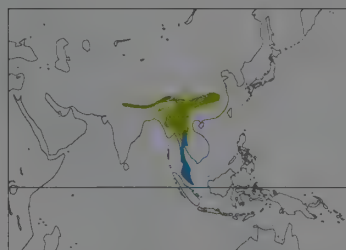
A. b. rogersi (Deignan, 1955) - E Myanmar, W Thailand and N Laos; winters as far S as Surat Thani (S Thailand).

A. b. vulcanorum (Stresemann, 1926) - mountains in W Java.

Descriptive notes. 13-14 cm. Large swiftlet with obviously forked tail; grey rump band clearly paler than dark brown upperparts; underparts very uniform pale grey; lightly feathered tarsi and white rami. Race *innominatus* has darker rump than nominate; *rogersi* smallest race, similar to nominate but lacking white rami and tarsus feathering; *vulcanorum* has darker underparts and obvious pale rump, male with bare tarsi. Capable of echolocation.

Habitat. Primarily in highlands, particularly over wooded river valleys, though not uncommon over wide range of habitats, including cultivated areas. Recorded to 4575 m in Nepal and between 1500-2800 m in C Bhutan. Race *vulcanorum* not recorded away from highland habitats, notably rims of volcanic craters.

Food and Feeding. Diptera and Hymenoptera recorded. Gregarious, typically up to 50; larger flocks, e.g. 300, not uncommon. Associates with other swifts and hirundines. Often descends from hills in evenings or during poor weather to forage over cultivated land, particularly paddies, where areas of standing water especially favoured.



Breeding. Season Apr-Jun, India; eggs collected late Apr, Shan States, Myanmar. Colonial. Nests on vertical rock-faces, inside caves or similar structures; self-supporting bracket-shaped nest of vegetable materials agglutinated with sparse, but firm, saliva. Copulation noted at nest and in air; 2 eggs.

Movements. Partial migrant, with apparently only relatively small proportions of populations moving S for winter. Recorded Nov-Mar in Malay Peninsula. Nocturnal migrants recorded in Nov at Fraser's Hill, W Malaysia, were nominate race or *innominatus*. In Strait of Malacca, 4 on passage through Riau Archipelago

in mid-Sept to early Oct, and 3 of indeterminate race collected in Nov from lighthouse; believed to be common passage migrant on Karimun Besar. Status in Sumatra uncertain, where in past reported to be a breeding resident, but may be merely winter visitor or straggler; large southward movement of c. 2860 swiftlets over S Serkap in early Oct probably refers to this species. Nominate race is altitudinal migrant in parts of Himalayas, wintering at 900-2750 m in Nepal; a few records from NE Bangladesh, where species may be only irregular winter visitor. Type specimen of race *innominatus* from S Andamans, where species is probably only rare straggler in winter. Race *vulcanorum* strictly resident. Race *rogersi* not known with certainty S of Surat Thani; has been recorded in SW Yunnan (SC China).

Status and Conservation. Not globally threatened. Common throughout most of breeding range, though is an uncommon wintering species in Malay Peninsula; rather rare in China; recorded as a rare winter visitor in New Forest, Dehra Dun, N India; in suitable habitat, for instance in N Thailand, species can be abundant, and is especially obvious around dusk; first records for W Myanmar as recently as 1994. Race *vulcanorum* sometimes considered full species and classified as Vulnerable; also as restricted-range species, present in Java and Bali Forests EBA; all recent records from 1 site, Gunung Gede, where species is not always seen by visiting ornithologists; it has been suggested that active volcanoes around which it occurs occasionally cause localized extinction; this threat, together with scarcity of suitable breeding habitat, suggests that this form has always been rare and would present considerable problems for conservation management.

Bibliography. Ali & Ripley (1983), Ali *et al.* (1996), Bangs & Van Tyne (1931), Cheng Tsohsin (1983), Clayton *et al.* (1996), Collar *et al.* (1994), David-Beaulieu (1994), Deignan (1945, 1955b), Étchécopar & Hue (1978), Fan Zhiyong & He Feng (1997), Glennie (1944), Grimmett *et al.* (1998), Hale & Kennerley (1994), Holmes (1996), Inskipp *et al.* (1996), Lee *et al.* (1996), Lekagul & Round (1991), Li Dewu *et al.* (1981), MacKinnon & Phillips (1993), van Marle & Voous (1988), Medway (1966), Medway & Pye (1977), Medway & Wells (1976), Mohan (1997), Ollington & Loh (1996), Pratt (1986), Riley (1938), Ripley (1982), Robson (1995a, 1997a), Robson *et al.* (1998), Salomonsen (1983), Smythies (1986), Somadikarta (1967), Stattersfield *et al.* (1998), Stresemann (1931a), Tymstra *et al.* (1997), Wells (1999), Xiong Tieyi (1988), Zhao Zhengjie (1995).

PLATE 39

inches

5

cm

13



27. Whitehead's Swiftlet

Aerodramus whiteheadi

French: Salangane de Whitehead

Spanish: Salangana de Whitehead

German: Philippinensalangane

Other common names: Whitehead's Mountain Swiftlet

Taxonomy. *Collocalia whiteheadi* Ogilvie-Grant, 1895, Mount Data, Luzon. Genus often merged into *Collocalia*. In past considered conspecific with *A. orientalis*, but apparently not closely related. Formerly linked with *A. brevirostris*, but differs in nest type and rump pattern. Has also been considered conspecific with *A. papuensis*, but does not lack fourth toe. Two forms previously listed as races of present species have now been synonymized with other congeneric taxa: *tsubame* with *A. vanikorensis palawanensis*; and *apoensis* with *A. mearnsi*. Many old records attributed to this species actually refer to *A. vanikorensis amelis*. Two subspecies recognized.

Subspecies and Distribution.

A. w. whiteheadi (Ogilvie-Grant, 1895) - Mt Data on Luzon (N Philippines).

A. w. originis (Oberholser, 1906) - Mt Apo on Mindanao (S Philippines).



Descriptive notes. 14 cm. Large swiftlet with massive head and deep tail-fork; black-brown upperparts with some white rami but lacking paler rump; extensive pale fringing to lores and over eye; paler brown underparts; naked tarsi. Race *originis* darker above and below. No information available as to whether or not species is capable of echolocation.

Habitat. Recorded only from naturally forested, montane sites.

Food and Feeding. Not known.

Breeding. Nestling and nests collected from Mt Apo early Jul, where 4 rounded nests found in hollow tree, consisting of green bryophytes

with fibrous vegetable matter but apparently lacking saliva nest-cement, are considered by some to have been made by *originis*.

Movements. Presumed resident.

Status and Conservation. VULNERABLE. Restricted-range species: present in Luzon EBA and Mindanao and the Eastern Visayas EBA. Clearly in need of further study. Recent specimens collected from S Cotabato, Mindanao, may or may not relate to records from Mt Matutum in Nov 1993. May be at risk from habitat loss.

Bibliography. Anon. (1997b), Clayton *et al.* (1996), Collar *et al.* (1994), Delacour & Mayr (1946), Dickinson (1989a), Dickinson *et al.* (1991), Inskipp *et al.* (1996), McGregor (1904), Medway (1966), Oberholser (1906), Ogilvie-Grant (1895), Poulsen (1995), Pratt (1986), Salomonsen (1983), Somadikarta (1967), Stattersfield *et al.* (1998), Stresemann (1914a, 1914b, 1926).

28. Bare-legged Swiftlet

Aerodramus nudatarsus

French: Salangane de Salomonsen

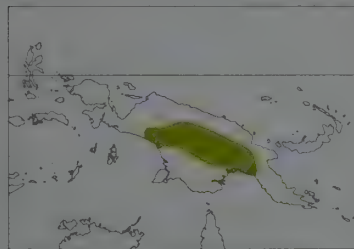
Spanish: Salangana Tarsidesnuda

German: Nacktfußsalangane

Other common names: Schrader Mountain/New Guinea/Naked-legged Swiftlet

Taxonomy. *Collocalia nudatarsus* Salomonsen, 1963, Baroka, Bioto Creek, New Guinea. Genus often merged into *Collocalia*. Sometimes treated as forming a superspecies with *A. orientalis*, and thence also linked with *A. whiteheadi*. Monotypic.

Distribution. S & SE New Guinea. May breed N of central watershed in Schrader Range.



Descriptive notes. 14 cm. Large swiftlet with shallow tail-fork; dark brown above, rump uniform, with extensive pale fringes on lores and over eye; uniformly sooty-grey underparts; apparently some variation in rami colouring. Bare tarsi, glossless upperparts and presence of 4 toes distinguish present species from *A. papuensis*. No information available as to whether or not species is capable of echolocation.

Habitat. Collected mainly in highlands, though also as low as 30 m above sea-level.

Food and Feeding. Not known.

Breeding. No information available.

Movements. Resident.

Status and Conservation. Not globally threatened. Restricted-range species: present in Central Papuan Mountains EBA. Believed to be uncommon, and certainly species is relatively uncommon in museum collections. Biology and ecology almost totally unknown; extensive research required.

Bibliography. Beehler *et al.* (1986), Coates (1985), Diamond (1972), Pratt (1986), Rand & Gilliard (1967), Salomonsen (1962, 1983), Somadikarta (1967), Stattersfield *et al.* (1998).

29. Mayr's Swiftlet

Aerodramus orientalis

French: Salangane de Mayr

German: Salomonensalangane

Spanish: Salangana de Guadalcanal

Other common names: Guadalcanal Swiftlet

Taxonomy. *Collocalia lowi orientalis* Mayr, 1935, Guadalcanal, Solomon Islands.

Genus often merged into *Collocalia*. Sometimes treated as forming a superspecies with *A. nudatarsus*. Formerly considered conspecific with *A. whiteheadi*. A specimen from Bougainville

I was intermediate in size between nominate and race *leletensis*; although some plumage details were rather different, it was provisionally thought to belong within this species. Two subspecies currently recognized.

Subspecies and Distribution.

A. o. leletensis Salomonsen, 1963 - C New Ireland.

A. o. orientalis Mayr, 1935 - Guadalcanal (Solomon Is.).

Also known from Bougainville I, though taxonomic assignment of the only specimen requires further investigation.



Descriptive notes. 13-14 cm. Large swiftlet with proportionally short tail and shallow tail-fork; black upperparts with broad, pale grey rump, pale fringes to lores and over eye; uniformly sooty-brown underparts; thinly feathered tarsi. Race *leletensis* has glossy blue-black upperparts, slightly darker and narrower rump-band and naked tarsi. No information available as to whether or not species is capable of echolocation.

Habitat. Not well known, but assumed to be a highland species.

Food and Feeding. Not known.

Breeding. No information.

Movements. Apparently resident, though very little known.

Status and Conservation. Not globally threatened. Restricted-range species: present in New Britain and New Ireland EBA and Solomon Group EBA. Data-deficient. Known with certainty only from 2 specimens, collected in 1935 on Guadalcanal and in 1962 on New Ireland. Sightings of unidentified large swiftlets on New Georgia in Jul 1987 and on Manus in May 1989, coupled with Bougainville specimen of Jun 1979, suggest that this species may prove to have a more extensive range than currently thought; survey work required, as is research into basic biology of species.

Bibliography. Blaber (1990), Coates (1985), Collar *et al.* (1994), Hicks (1992a), Pratt (1986), Ripley (1983), Salomonsen (1962, 1983), Somadikarta (1967), Stattersfield *et al.* (1998).

30. Mossy-nest Swiftlet

Aerodramus salangana

French: Salangane de la Sonde

German: Moosnestsalangane

Spanish: Salangana de la Sonda

Other common names: Mossy/Sunda Swiftlet

Taxonomy. *Hemiprocne salangana* Streubel, 1848, Java.

Genus often merged into *Collocalia*. Forms superspecies with *A. vanikorensis*, *A. pelewensis*, *A. bartschi* and *A. inquietus*; all were formerly considered conspecific. Race *aerophilus* of doubtful validity; often placed in *A. fuciphagus*. Races *A. vanikorensis aenigma* and *A. v. heinrichi* sometimes considered to belong to present species. Four subspecies recognized.

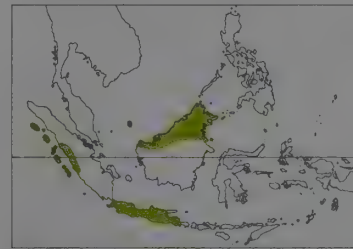
Subspecies and Distribution.

A. s. natunae (Stresemann, 1930) - N Borneo, and probably Sumatra and Natuna Is.

A. s. maratua (Riley, 1927) - Maratua Archipelago (off NE Borneo).

A. s. aerophilus (Oberholser, 1912) - islands off W Sumatra, including Nias.

A. s. salangana (Streubel, 1848) - Java.



Descriptive notes. 12 cm; 23 g. Medium-sized swiftlet with shallow tail-fork; uniform black-brown upperparts; uniform pale brown underparts. Race *natunae* averages longer-winged and has feathered tarsi; *maratua* and *aerophilus* smaller than other 2 races, *maratua* averaging paler than *aerophilus* which has deepest tail-fork (11-13%) and naked tarsi. From sympatrics only safely distinguishable in hand or on nest; tarsal feathering variable, very light or lacking in nominate; light shaft streaking on underparts, lacking in some; grey-brown rami to back feathers. Nominat and race *natunae* both capable of echolocation.

Habitat. Feeds over variety of habitats adjacent to breeding caves. Apparently feeds at lower levels and closer to nest than sympatric *A. maximus* and for shorter periods, though both feed together at swarms. Particularly favours caves in primary forest.

Food and Feeding. At Niah, Sarawak, 22 families and subfamilies of insects taken, certain beetles and swarming ants and termites predominating. Highly gregarious, associating with congeners and most active during crepuscular period. Feeds both amidst forest canopy and at lower elevations.

Breeding. Certain active colony studied Mar. Padang Highlands, Sumatra, and further probable record of active colony in limestone cave with *A. maximus* in Apr in same highlands; at Niah, breeds over 8 months from Sept to Apr. Colonial cave nester. Nest of vegetable matter agglutinated with sparse transparent saliva which remains soft and moist; requires support by ledge or similar irregularity. Two eggs, though 1 recorded; interval 2 days; both sexes brood but replacement of brooding bird does not occur during day; replacement and second clutches recorded; incubation period 19-27 days, mean 23. Fledging period where both young survived, 41-56 days, mean 48-5, compared with 41-55, mean 48, where only 1 survived after 2 hatched; young fed several times daily. Average breeding success 38% with 0.8 young fledged per breeding effort.

Movements. Presumed resident. Single record from Philippines (Basilan) suggests some degree of dispersal.

Status and Conservation. Not globally threatened. Believed to be uncommon on Java, though identification problems may disguise true status; otherwise locally abundant. Occurs in Gunung Mulu National Park, Sarawak; range might extend to S half of Borneo.

Bibliography. Chapman (1985), Clayton *et al.* (1996), Cranbrook (1984), Dickinson (1989a), Dickinson *et al.* (1991), Harrison (1974), Hellebrekers & Hoogerwerf (1967), Inskipp *et al.* (1996), Lee *et al.* (1996), MacKinnon (1988), MacKinnon & Phillips (1993), van Marle & Vovus (1988), Medway (1961, 1962a, 1962b, 1966), Oberholser

(1932), Pratt (1986), Riley (1927), Robinson & Kloss (1924), Salomonsen (1983), Seitre, J. & Seitre (1991), Seitre, R. & Seitre (1992), Smythies (1981), Wells (1975).

31. Uniform Swiftlet

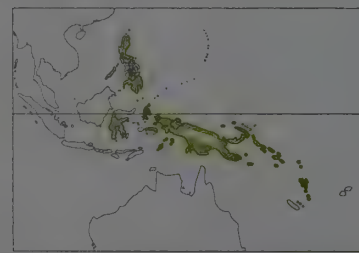
Aerodramus vanikorensis

French: Salangane de Vanikoro **German:** Einfarbsalangane **Spanish:** Salangana de Vanikoro
Other common names: Island/Lowland/Vanikoro Swiftlet; Grey/Philippine Swiftlet(!) (*amelis*); Palawan Swiftlet (*palawanensis*)

Taxonomy. *Hirundo vanikorensis* Quoy and Gaimard, 1830, Island of Vanikoro. Genus often merged into *Collocalia*. Forms superspecies with *A. salangana*, *A. pelewensis*, *A. bartschi* and *A. inquietus*; all were formerly considered conspecific; *A. mearnsi* was previously included in this superspecies too. Both *A. infuscatus* and *A. hirundinaceus* have been treated as races of present species. Races *palawanensis* and *amelis* sometimes considered two (or one) distinct species; former has been treated as conspecific with *A. maximus* or *A. whiteheadi*, and latter with *A. fuciphagus*. Races *aenigma* and *heinrichi* sometimes considered to belong to *A. salangana*. Population on Yamdena in Tanimbar Is not yet subspecifically assigned and may belong to an undescribed race. Australian birds formerly treated alone as race *yorki*, with name *granti* applied to New Guinea birds; however, the only two Australian records refer to vagrants identical to the New Guinea form, and it is clear that only a single race is involved; this race often listed as *granti*, but name *yorki* has priority by 21 years. Proposed race *isubame* of *A. whiteheadi* now considered a synonym of race *palawanensis*. Fourteen subspecies currently recognized.

Subspecies and Distribution.

A. v. amelis (Oberholser, 1906) - Luzon, Mindoro, Cebu, Bohol and Mindanao (E Philippines).
A. v. palawanensis (Stresemann, 1914) - Palawan (SW Philippines).
A. v. aenigma (Riley, 1918) - C Sulawesi.
A. v. heinrichi (Stresemann, 1932) - Sulawesi.
A. v. moluccarum (Stresemann, 1914) - Seram, Ambon, Banda, Gorong, Tayandu and Kai Is (S Moluccas).
A. v. waigeuensis (Stresemann & Paludan, 1932) - N Moluccas (Morotai, Halmahera) and W Papuan Is (Misool, Batanta, Waigeo and probably Salawati).
A. v. steini (Stresemann & Paludan, 1932) - Biak and Numfor (in Geelvink Bay, NW New Guinea).
A. v. yorki (Mathews, 1916) - Aru Is, New Guinea and D'Entrecasteaux Is.
A. v. tagulae (Mayr, 1937) - Louisiade Archipelago, Trobriand Is and Woodlark I.
A. v. coultasi (Mayr, 1937) - Admiralty Is (Manus, Rambutuy, Los Negros) and St Matthias group.
A. v. pallens (Salomonsen, 1983) - New Hanover, New Ireland and nearby Djaul I, and New Britain.
A. v. lihiensis (Mayr, 1937) - Nuguria and Hibernian Is, Tabar Is, Lihir group and Feni Is (E of New Ireland).
A. v. lugubris (Salomonsen, 1983) - Solomon Is.
A. v. vanikorensis (Quoy & Gaimard, 1830) - Santa Cruz Is (including Duff Is and Swallow Is) and Vanuatu.
Also (subspecies unknown) Yamdena in Tanimbar Is.



Descriptive notes. 13 cm. Medium-sized swiftlet with moderately forked tail; grey-brown above; slightly darker undertail-coverts on otherwise pale grey-brown underparts; limited darker shaft-streaking. Highly variable, with rump uniform with upperparts in all races except *pallens* which has at best an indistinctly paler rump. Philippine races separable from each other on wing length, *amelis* shorter than *palawanensis*; *aenigma* dark, blackish above with blue-green gloss and dark grey-brown below, with extensive white rami to rump area; *heinrichi* paler below and green-glossed above; *moluccarum* as *aenigma* with larger eye-patch

and greater fringing on undertail-coverts; small *waigeuensis* darker than *aenigma* but with paler throat and upper breast, lacking dark shaft streaks; *steini* larger and darker than *waigeuensis*; *granti* blacker above with paler throat and relatively short tail; *tagulae* with paler underparts and darker throat than nominate; *pallens* darker above than *tagulae* with extensive white rami and hence pale rump and whitish throat; *coultsi* paler above than *pallens*; *lugubris* uniformly blackish above with white rami absent or much reduced and underparts dark grey; *lihiensis* intermediate between latter 2 forms. Capable of echolocation.

Habitat. Occurs over variety of habitats, mainly forest, including coasts and islands, from lowlands to over 500 m on Sulawesi and 700 m on Seram. Found from lowlands to highlands, New Guinea to 1400 m and Goodenough I to 1600 m. On Santa Isabel mainly in lowlands, to 900 m over gardens and second-growth. In lowland rainforest zone of Papua New Guinea recorded over forest, forest edge and non-forest.

Food and Feeding. Highly gregarious, associating with congeners. Highly transient when foraging. Feeds at lowest elevations when over open country; feeds throughout day but still active at dusk. Insect prey size 1-6 mm recorded in Bismarck Archipelago.

Breeding. Season Aug-Dec, sometimes to Feb. Vanuatu; breeding New Guinea at Musgrave R and Mafulu, both Central Province, in Aug and Oct respectively, and on Goodenough I in Oct; breeds in Jun on Luzon, Philippines. Colonial. Typically nests in total darkness in cave or similar structure; 1 nest noted under overhanging bank of earth on side of stream. Described nests tend to be rounded, though bracket-like, composed of strands of vegetable matter and agglutinated with moderate to sparse amount of saliva; some have at least partial support. Clutch 1-2.

Movements. Resident, but with some evidence of local movements. Numbers known to fluctuate in some places, e.g. at Waigani Bay (SE New Guinea) with increase Nov-Dec but decrease in Feb. Vagrant to Queensland (NE Australia), with two confirmed records (one producing type specimen of race *yorki*) and several more reports of possible sightings. Often moves along fronts of storms.

Status and Conservation. Not globally threatened. Common to abundant throughout range. Reported as common in C Sulawesi in early 1980's. Occurs in several protected areas throughout range, e.g. in Philippines: *palawanensis* in Saint Paul Subterranean National Park, Palawan; and *amelis* in Rajah Sikatuna National Park, Bohol. Race *palawanensis* sometimes considered full species and classified as restricted-range species; present in Palawan EBA.

Bibliography. Bechler, Pratt & Zimmerman (1986), Bechler, Sengo *et al.* (1995), Blaber (1990), Bravery (1971, 1973), Bregulla (1992), Brooks *et al.* (1996), Browning (1993), Cain & Galbraith (1956), Clayton *et al.* (1996),

Coates (1985), Coates & Bishop (1997), Coleman (1981), Collins & Murphy (1993), Danielsen *et al.* (1994), Dickinson (1989a), Dickinson, Kennedy & Parkes (1991), Dickinson, Kennedy, Read & Rozendaal (1989), Evans, Magsalay *et al.* (1993), Finch & McKean (1987), Gregory (1995a, 1995b), Higgins (1999), Inskipp *et al.* (1996), Isherwood *et al.* (1997), Lambert (1994), LeCroy & Peckover (1983), Manuel (1937), Mayr (1937a, 1945), Mayr & van Deusen (1956), Mayr & Rand (1937), Medway (1966, 1975b), Medway & Pye (1977), Mees (1965), Oberholser (1906), Pratt (1986), Rabor (1954), Rand & Gilliard (1967), Rand & Rabor (1960), Ripley (1964a), Robson (1996a, 1997a), Salomonsen (1983), Schodde & Mason (1997), Schodde & McKean (1972), Stattersfield *et al.* (1998), Stresemann (1922, 1932, 1940), Stresemann & Paludan (1932), Tubb (1945), Watling (1983), Webb (1992), Wells (1975), White & Bruce (1986).

32. Palau Swiftlet

Aerodramus pelewensis

French: Salangane des Palau **German:** Palausalangane **Spanish:** Salangana de las Palau

Taxonomy. *Collocalia pelewensis* Mayr, 1935, Palau Islands.

Genus often merged into *Collocalia*. Forms superspecies with *A. salangana*, *A. vanikorensis*, *A. bartschi* and *A. inquietus*; all were formerly considered conspecific. Previously placed in *A. bartschi*, and sometimes also associated with *A. fuciphagus germani* and *A. f. inexpectatus*. Monotypic.

Distribution. Palau Is.



Descriptive notes. 11 cm. Small swiftlet with relatively short, moderately forked tail; black-brown upperparts with grey-brown rump; underparts palest on throat, darkest on undertail-coverts, rest dull grey; shaft streaks most distinct on undertail-coverts; lacks supraloral spot and tarsal feathering. From other Micronesian swiftlets by pale rump, and from *A. bartschi* by more glossy black plumage, greyer ventrally on underparts, and longer wings; both *A. bartschi* and *A. inquietus* have a shallower tail-fork. Available information suggests species probably capable of echolocation.

Habitat. Occurs on larger islands of group. Most numerous flocks typically over highland ridges and gorges, shying from deep forest.

Food and Feeding. Most active at dusk when forms largest flocks. Small flocks forage in a restricted area for long periods during day.

Breeding. Active colony on Malakal I in mid-Oct. Colonial, nesting in caves. Very flat nests attached to cave roof are lined with moss and fine grass; 95 mm wide x 35 mm deep, cup diameter 50 mm. 1 egg.

Movements. Resident.

Status and Conservation. Not globally threatened. Restricted-range species; present in Palau EBA. Common to abundant within small range, with no large population change noted between 1949 and 1988.

Bibliography. Baker (1951), Brandt (1966), Browning (1993), Engbring (1988), Marshall (1949), Mayr (1935, 1937a, 1945), Medway (1966, 1975b), Pratt (1986), Pratt, Bruner & Berrett (1987), Pratt, Engbring *et al.* (1980), Salomonsen (1983), Stattersfield *et al.* (1998).

33. Guam Swiftlet

Aerodramus bartschi

French: Salangane de Guam **German:** Marianensalangane **Spanish:** Salangana de Guam
Other common names: Micronesian(!)/Guam Cave/Mariana Swiftlet

Taxonomy. *Collocalia bartschi* Mearns, 1909, Guam.

Genus often merged into *Collocalia*. Forms superspecies with *A. salangana*, *A. vanikorensis*, *A. pelewensis* and *A. inquietus*; all were formerly considered conspecific. Previously lumped with *A. pelewensis*, and sometimes also associated with *A. fuciphagus germani* and *A. f. inexpectatus*. Considered a race of *A. inquietus* by some authors. Monotypic.

Distribution. Saipan, Tinian and Guam in S Mariana Is. Introduced to Oahu, Hawaii.



Descriptive notes. 11 cm. A small swiftlet with a moderately forked tail; warm brown upperparts lacking sheen and with uniform rump; underparts darker grey beneath silver-grey throat; tarsi bare or lightly feathered; supraloral patch missing or much reduced; underparts lack shaft streaks. Notably paler than *A. inquietus*. Available information suggests the species is probably capable of echolocation.

Habitat. Occurs over a wide range of cleared and forested habitats in interior and on coast, including mangroves.

Food and Feeding. Tends to be most noticeable

gregarious in evenings when large groups feed very low, not moving up and away until nightfall. Feeding times and habits similar to those of sympatrically occurring sheath-tailed bats (*Emballonura*).

Breeding. Active colonies Mar-May. Colonial, up to 250 nests with clusters of 25-50. Nest cylindrical, birds adding to it each season, supported by niche in cave wall; composed of moss agglutinated by large amounts of hardened saliva.

Movements. Nomadic movements account for occasional temporary gatherings at dusk or for longer periods, and absence from certain islands.

Status and Conservation. Not globally threatened. Restricted-range species; present in Mariana Islands EBA. Marked decline seems apparent since species was recorded as abundant on both Guam and Saipan in 1949. By 1987, it had become extinct on Rota, was approaching extinction on Guam and was uncommon on Saipan, Tinian and Agiguan; conservation status probably requires reassessment; surveys needed. Introduced to Oahu, Hawaii, in 1962, and now breeds in Halawa and Moanalua Valleys, although population appears to be very small; 12 pairs found breeding in 1989.

Bibliography. Anon. (1991, 1998a), Baker (1951), Brandt (1966), Browning (1993), Jenkins (1979, 1983), Lee *et al.* (1996), Marshall (1949), Mayr (1937a, 1945), Mearns (1909b), Medway (1966), Pratt (1986), Pratt *et al.* (1979, 1987), Stophlet (1946), White, T. (1996).

34. Caroline Swiftlet

Aerodramus inquietus

French: Salangane des Carolines **German:** Karolinsensalangane **Spanish:** Salangana de las Carolinas
Other common names: Micronesian Swiftlet(!)

Taxonomy. *Cypselus inquietus* Kittlitz, 1858, Kosrae, Caroline Islands. Genus often merged into *Collocalia*. Forms superspecies with *A. salangana*, *A. vanikorensis*, *A. pelewenis* and *A. bartschi*; all were formerly considered conspecific. Considered conspecific with *A. bartschi* by some authors. Three subspecies recognized.

Subspecies and Distribution.

A. i. rukensis (Kuroda, 1915) - Chuuk (C Caroline Is).
A. i. ponapensis (Mayr, 1935) - Pohnpei (E Caroline Is).
A. i. inquietus (Kittlitz, 1858) - Kosrae (E Caroline Is).



Descriptive notes. 11 cm. Small swiftlet with moderately forked tail, shallower than in *A. pelewenis*; underparts uniformly dark grey-brown. Race *ponapensis* has black-brown upperparts with faint green gloss and can show slightly paler rump; *rukensis* has slightly shorter wing. Uncertain whether or not species is capable of echolocation.

Habitat. Occurs over both open and forested habitats.

Food and Feeding. Virtually nothing known; assumed to be similar to congeners.

Breeding. Active colony with eggs in various stages of incubation Kosrae, mid-May;

eggs collected Jokaz, Apr. May and Aug. during 1958 and 1959; eggs recorded Chuuk, Apr. May, Jul, Sept, Nov and Dec. Colonial. Race *rukensis* nests in total darkness, nominate race and *ponapensis* in less dark situations. Nest of *rukensis* deeply cupped, firmly attached to cave wall, of vegetable matter and some feathers agglutinated with large amounts of saliva; *ponapensis* typically nests in clusters, making distinctly rounded, bracket-type nest of moss and soft vegetable matter with saliva used only at point of attachment to cave wall. Race *rukensis* lays 2 eggs, nominate race and *ponapensis* only 1.

Movements. Resident.

Status and Conservation. Not globally threatened. Restricted-range species: present in East Caroline Islands EBA. Common to abundant. Population estimates of 27,900 birds on Kosrae, 29,800 on Pohnpei and 25,800 on Chuuk, published 1993. Status on Yap I uncertain, whence there is a 19th-century sighting of a swiftlet species.

Bibliography. Baker (1951), Brandt (1962, 1966), Browning (1993), Mayr (1935, 1945), Medway (1966), Pratt (1986), Pyle & Engbring (1985), Ralph & Sakai (1979), Stattersfield *et al.* (1998).

35. Atiu Swiftlet

Aerodramus sawtelli

French: Salangane de Cook **German:** Atiusalangane **Spanish:** Salangana de las Cook
Other common names: Cook (Islands)/Sawtelli's Swiftlet

Taxonomy. *Aerodramus sawtelli* Holyoak, 1974, Atiu Island.

Genus often merged into *Collocalia*. Has been considered to form a superspecies with *A. leucophaeus*, or even to be conspecific, but apparently differs in nest habits. May prove to be merely a race of *A. spodiopygius*, which is very similar in size and plumage and which occurs not far from Cook Is. Monotypic.

Distribution. Atiu I (S Cook Is).



Descriptive notes. 10 cm. Small to medium-sized swiftlet with relatively long, forked tail; black-brown upperparts with contrastingly pale grey rump; pale grey-brown underparts appearing darkest on undertail-coverts; pale supraloral patch reduced or missing. Separable from *A. leucophaeus leucophaeus* by smaller size, shorter tail, paler bases to uppertail-coverts, paler underparts and different bill structure; *A. l. ocistus* somewhat intermediate. Capable of echolocation.

Habitat. Occurs over both open and forested habitats.

Food and Feeding. Little known. Forages

slowly amidst forest canopy and along forest margins.

Breeding. Most nests built Sept with last chicks fledged Apr. Colonial cave breeder. Nest typically bracket-and-cup-shaped and self-supporting using a small quantity of saliva, though those on ledges had cups supported upon a base. Nest composed primarily of plant material, mostly coconut crown fibre and lichens with lesser quantities of *Casuarina* needles, grass, angiosperm leaves and passion-fruit (*Passiflora*) tendrils; other components include feathers from this species and less commonly its own eggshells and flowers of *Ocimum gratissimum*. Two eggs, both sexes incubating; sometimes 2 broods. Average weight of young 1.1 g at hatching and 9.5 g when they fledge; fledging period averages 53 days.

Movements. Resident.

Status and Conservation. VULNERABLE. Restricted-range species: present in Southern Cook Islands EBA. No decline apparent to date. There were thought to be only 60 nests when species was first discovered in 1973. Census in 1987-1988 recorded 190 active nests in two caves; in addition, other smaller colonies are believed to exist. Recent studies show density of 1 breeding bird per 7 ha, equivalent to total of 380 breeding birds on the island. Crab predation and starvation after falling from nest are main causes of fledgling mortality. Tourist disturbance may pose future problem.

Bibliography. Collar & Andrew (1988), Collar *et al.* (1994), Fullard *et al.* (1993), Holyoak (1974a, 1980), Holyoak & Thibault (1978, 1984), Lee *et al.* (1996), Mayr & Vuilleumier (1983), McCormack (1997), Medway & Pye (1977), Pratt (1986), Pratt *et al.* (1987), Stattersfield *et al.* (1998), Tarburton (1990a)

36. Polynesian Swiftlet

Aerodramus leucophaeus

French: Salangane de la Société **German:** Polynesiensalangane **Spanish:** Salangana Polinesia
Other common names: South Pacific Swiftlet; Tahiti/Tahitian Swiftlet (*leucophaeus*); Marquesas/Marquesan Swiftlet (*ocistus*)

Taxonomy. *Macropteryx leucophaeus* Peale, 1848, Tahiti.

Genus often merged into *Collocalia*. Has been considered to form a superspecies with *A. sawtelli*, or even to be conspecific, but apparently differs in nest habits. Race *ocistus* (with *gilliardi*) sometimes considered a distinct species, being intermediate in some features between nominate race and *A. sawtelli*. Variation in relative pallor of rump within birds of Tahitian population led to past recognition of pale-rumped race "thespesius", but this is now considered to fall within normal variation of nominate race. Three subspecies currently recognized.

Subspecies and Distribution.

A. l. leucophaeus (Peale, 1848) - Moorea and Tahiti (E Society Is).
A. l. ocistus (Oberholser, 1906) - Eiao, Nuku Hiva and Ua Huka (N Marquesas).
A. l. gilliardi (Somadikarta, 1994) - Ua Pu, Hiva Oa and Tahuata (S Marquesas).



Descriptive notes. 11 cm. Medium-sized swiftlet with proportionally long, forked tail; plumage appears rather uniform: dark-brown upperparts with grey rump, which may be paler ("thespesius") or darker; grey-brown underparts. Less contrast between upperparts and underparts than in *A. sawtelli*, which has paler underparts. Races *ocistus* and *gilliardi* somewhat intermediate between nominate race and *A. sawtelli* and differ further from both in proportionally longer tail; race *gilliardi* differs from *ocistus* in having naked tarsi, slightly longer wings and tail, and slightly deeper tail-fork. Race *ocistus* (and presumably *gilliardi*)

capable of echolocation; nominate unknown.

Habitat. Occurs over riverine habitats, rocky valleys and humid forests.

Food and Feeding. Race *ocistus* apparently more gregarious than nominate race, perhaps due to larger size of population. Nominat feeds at high elevations over range of habitats recorded for species, while *ocistus* apparently forages slowly amidst forest canopies and margins.

Breeding. Nests collected Marquesas in Oct. Colonial, up to 300 birds reported. Wide variety of nest-sites: caves, deep or shallow, depressions under rocks or coastal cliffs. Self-supported or externally supported nest of vegetable matter agglutinated with sparse, sticky saliva. 2 eggs.

Movements. Resident, but may be only vagrant to Moorea, suggesting that some dispersal might occur.

Status and Conservation. Not globally threatened. When treated as two distinct species both forms are restricted-range species: *leucophaeus* present in Society Islands EBA; *ocistus* present in Marquesas Islands EBA. Nominat *leucophaeus* classed as Vulnerable; has declined in 20th century possibly as a result of predation on chicks and eggs by introduced Common Mynas (*Acridotheres tristis*); found in only 6 of 39 Tahitian valleys during surveys of 1986-1991; total population estimate of 200-500 birds in 1984; extinct on Huahine, easternmost of W Society Is. Other races common on most islands in Marquesas, but not on Hiva Oa, where may also suffer from presence of introduced Common Myna.

Bibliography. Berlioz (1929b), Clayton *et al.* (1996), Collar & Andrew (1988), Collar *et al.* (1994), Fisher & Wetmore (1931), Holyoak (1974b, 1975), Holyoak & Thibault (1978, 1984), Medway (1966), Medway & Pye (1977), Monnet *et al.* (1993), Oberholser (1906), Pratt (1986), Pratt *et al.* (1987), Salomonsen (1983), Somadikarta (1994), Stattersfield *et al.* (1998), Thibault (1988), Thibault & Rives (1988).

37. Black-nest Swiftlet

Aerodramus maximus

French: Salangane à nid noir **German:** Schwarzneestsalangane **Spanish:** Salangana Nidonegro
Other common names: Indo-Malayan Swiftlet; Robinson's Swiftlet (*maximus*); Lowe's Swiftlet (*lowi*)

Taxonomy. *Collocalia maxima* Hume, 1878, Tenasserim.

Genus often merged into *Collocalia*. Much confusion over nomenclature: species originally named *maxima* in 1876, but incorrectly: validated by same author in 1878; however, this emendation was long overlooked, in part due to lumping of these names within *A. brevirostris innotatus*, an older name; during this period name used for present species was *lowi*, while northern race was listed as *robinsoni*, as next available name. Despite the unlikely distribution pattern resulting, nominate race and *lowi* apparently co-occur and intergrade in W Java. Both *A. brevirostris vulcanorum* and *A. vanikorensis palawanensis* have been placed in present species. Three subspecies recognized.

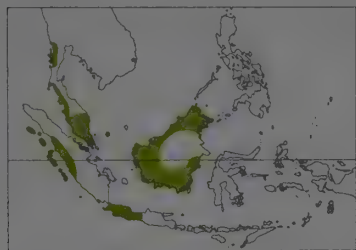
Subspecies and Distribution.

A. m. maximus (Hume, 1878) - S Myanmar to S Malay Peninsula, SE Vietnam and W Java.
A. m. lowi (Sharpe, 1879) - Sumatra and islands off W coast, N, W & S Borneo, Labuan I and W Java.
A. m. tichelmani (Stresemann, 1926) - SE Borneo.

Descriptive notes. 12-14 cm; 28 g. Medium-sized to large swiftlet with comparatively shallow tail-fork; glossy black-brown upperparts with typically uniform rump, though some have greyish rump; underparts grey, palest on throat and darker from chest, becoming darkest on belly and undertail-coverts; rami of back dark-tipped with only traces of white. In hand averages longer than *A. salangana* or *A. fuciphagus*. Differs from *A. brevirostris* by heavy tarsal feathering and less deeply forked tail. Race *lowi* has darkest rump; *tichelmani* smallest, with rump similar to nominate. Both nominate and *lowi* capable of echolocation; *tichelmani* unknown.

Habitat. Occurs from lowlands to highlands over range of habitats, including dense forest where adjacent to breeding colonies.

Food and Feeding. At Niah, Sarawak, 14 insect families and subfamilies recorded, with ants, termites and certain beetles predominating. Takes advantage particularly of swarming insects. Apparently feeds at higher levels and farther from nest than sympatric *A. salangana* and for longer periods.



though both feed together at swarms. Highly gregarious, often flocking with congeners, most active in crepuscular period. It has been speculated that it may be able to feed on swarms in the dark, as some termites and ants swarm from sunset into full darkness.

Breeding. Eggs collected on Thai Peninsula, mid-Apr; active colony in Padang Highlands, Sumatra, Apr; builds nests above high-tide mark from Feb, some eggs laid from early Mar, in Mergui Archipelago, Myanmar; at Niah, breeds Sept-Apr in unfarmed sites, though occasionally outside this season. Colonial cave nester, often sharing caves with *A. fuciphagus*, *A.*

salangana and *Collocalia esculenta*. Self-supporting, bracket-shaped nest made of large amounts of firm translucent saliva and feathers from any part of plumage; nest-building takes from 35 to over 127 days. One egg; both sexes brood but changeover does not occur during day; replacement and second clutches recorded; incubation 24-32 days, mean 28. Fledging period 52-65 days, mean 58.5; nestling fed infrequently, in 2 nests just once and twice in 24 hours (chick dying in first case), but feeding always occurs when adults return to roost. Average breeding success 17% with 0.2 young fledged per breeding effort.

Movements. Resident, though vagrancy to Palawan suggests some dispersal.

Status and Conservation. Not globally threatened. Scarcest in Malay Peninsula. Elsewhere abundant, despite alarming decrease at some farmed caves, e.g. 150,000-298,000 birds estimated at Niah caves in early 1990's where over 1,500,000 pairs estimated as recently as 1959. In 1950's it was thought that over 500,000 eggs or nestlings of this species and next were lost in 1 cave alone due to harvesting. Recorded in Vietnam only on islets off coast of Khanh Hoa province since 1981, where there were 65 nests in 1994.

Bibliography. Ali & Ripley (1983), Ali *et al.* (1996), van Balen & Prentice (1997), Basir *et al.* (1996), Brandt (1966), Clayton *et al.* (1996), Cranbrook (1984), Davison (1997a), Deignan (1955a), Dickinson (1989a), Dickinson, Kennedy & Parkes (1991), Dickinson, Kennedy, Read & Rozendaal (1989), Good (1993), Good & Wong (1989), Harrison (1974), Holmes & van Balen (1996), Inskipp *et al.* (1996), Kang & Lee (1991), Kang *et al.* (1991), Kenneth *et al.* (1995), Krueger (1966), Lee, P.G. (1984), Lee, P.G. & Kang (1994), Lee, P.L.M. *et al.* (1996), Lekagul & Round (1991), MacKinnon & Philipps (1993), Mardiatuti (1996), Mardiatuti & Marnata (1996), Mardiatuti & Soehartono (1996), van Marle & Voous (1988), Medway (1961, 1962a, 1962b, 1962c, 1966, 1969), Medway & Pye (1977), Medway & Wells (1976), Nguyễn (1996), Pakpahan & Soehartono (1994), Riley (1938), Robinson & Kloss (1924), Sims (1959, 1961), Smythies (1981, 1986), Stresemann (1931a), Valli & Summers (1990), Wells (1999).

38. Edible-nest Swiftlet

Aerodramus fuciphagus

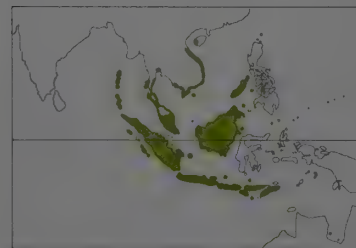
French: Salangane à nid blanc **German:** Weißnestsalangane **Spanish:** Salangana Nidoblanco
Other common names: Grey-rumped(!)/Hume's/White-nest Swiftlet; Andaman Grey-rumped Swiftlet (*inexpectatus*); German's/Oustalet's Swiftlet (*germani*); Brown-rumped Swiftlet(!) (*vestitus*); Thunberg's Swiftlet (*fuciphagus*)

Taxonomy. *Hirundo Fuciphaga* Thunberg, 1812, Java.

Genus often merged into *Collocalia*. In past, was at various times considered conspecific with many other swiftlet taxa, e.g. *A. francicus* and *A. unicolor*. Race *germani* sometimes considered a distinct species, often including *amechanus*. Races *dammermani* and *micans* often lumped within nominate, and still very poorly known. Proposed race *bartelsi* is synonym of nominate. *A. salangana* *aerophilus* often placed in present species. *A. vanikorensis amelis* has been linked with present species in a superspecies; race *perplexus* has been associated with *amelis*. Eight subspecies currently recognized.

Subspecies and Distribution.

- A. f. inexpectatus* (Hume, 1873) - Andaman and Nicobar Is.
- A. f. amechanus* (Oberholser, 1912) - Anambas Is (off SE Malay Peninsula).
- A. f. germani* (Oustalet, 1878) - coastline from W Hainan to Malay Peninsula, including Mergui Archipelago (off S Myanmar); coastal N Borneo and S Philippines (Palawan to Panay).
- A. f. vestitus* (Lesson, 1843) - Sumatra, Belitung and Borneo.
- A. f. perplexus* (Riley, 1927) - Maratua Archipelago (off E Borneo).
- A. f. fuciphagus* (Thunberg, 1812) - Java, Kangean Is and Bali to W Lesser Sundas and Tanahjampea.
- A. f. dammermani* (Rensch, 1931) - Flores.
- A. f. micans* (Stresemann, 1914) - Sumba, Sawu and Timor.



Descriptive notes. 12 cm; 15-18 g. Medium-sized swiftlet with relatively deeply forked tail; glossy, almost black-brown upperparts with rump typically appearing slightly greyer, though uniform in many; underparts palest and greyest on throat, rest browner grey except blackish undertail-coverts; lightly feathered or naked tarsi; white tips to rami, lacking in some individuals of nominate race and some of *vestitus*. Tail-fork 10-19% of tail length against under 13% in *A. maximus* and *A. salangana*. Race *inexpectatus* similar to nominate but averaging slightly smaller; *dammermani* apparently has slightly paler rump; *micans* paler and greyer with

slightly contrasting rump; *vestitus* has blackest upperparts, typically lacking rump contrast; *perplexus* has rather purple sheen to remiges and rectrices and slightly contrasting rump; *germani* has strikingly pale underparts and broad whitish rump; *amechanus* has greyer rump than *germani*. Nominative and races *amechanus*, *germani*, *vestitus* and *perplexus* all known to be capable of echolocation.

Habitat. Occurs over range of habitats, cleared and forested, coastal and interior, from sea-level to highlands, e.g. to 2800 m on Sumatra. Visits offshore islands and can be seen far out over sea.

Food and Feeding. Analysis of food balls from Penang, Malaysia, revealed following orders account for most prey items: Hymenoptera 41%, Ephemeroptera 26.5%, Homoptera 15.5% and Diptera 7.8%. These were collected during day, however, beetles and night-flying insects were under-represented. Mean foraging height over forested habitat, Malaysia, 57.5 m. Highly gregarious, often in large flocks including congeners, other swifts and hirundines. Most active in crepuscular period.

Breeding. Mainly Mar-Apr on Andaman and Nicobar Is; recorded early Dec, Tanahjampea 1 (N Flores Sea); begins nesting Mar, harvested for second time late Apr and again Jul, non-saliva

content increasing with each collection, peninsular Thailand; breeds Vietnam during first wet season in early Apr, nest-building in dry season Dec-Mar; breeds with *A. maximus*, starting to lay in Apr in Mergui Archipelago, Myanmar; believed to breed Jan-Jun, Palawan. In main study in Penang, breeding may occur year-round but egg-laying concentrated in Sept-Apr, most hatching Nov-Mar in dry season. Colonial, nesting in caves or similar structures, including purpose-built buildings; commonly breeds in urban areas. Nest bracket-shaped and self-supporting, made purely of opaque hardening saliva with extraneous matter rarely incorporated; nest-building takes 39-55 days. 2 eggs; incubation 25.5 days for first egg and 22.5 for second; fledging period 43 days. Hatching success 69%; average breeding success 49% with 0.9 young fledged per breeding effort.

Movements. Resident. Individuals breeding on smaller offshore islands may travel across sea to larger landmasses.

Status and Conservation. Not globally threatened. Abundant in suitable habitat, though declining in many areas as witnessed by reduced nest yields. In 1950's, it was thought that over half a million eggs or nestlings of this and the previous species were lost in 1 cave alone due to harvesting. In Nicobar Is, 1244-1791 pairs breed in 36 caves, and it is estimated that a population decline in excess of 85% has occurred during 1987-1995. Population of Vietnam estimated at c. 200,000 pairs; in decline, due to heavy overexploitation; recent studies, carried out with aim of trying to make harvesting less harmful, suggest limitation to two harvests per year, the first when only c. 10-15% of nests have eggs, and the second when fledglings of a second clutch have left their nests. Locally abundant on Flores and Timor but generally patchily distributed in Wallacea; two possible records from S Sulawesi. Race *germani* historically recorded from Laos, though these records may refer to *A. brevirostris rogersi* and cannot be considered reliable.

Bibliography. Abdulali (1978), Ali & Ripley (1983), Banks (1937), Basir *et al.* (1996), Brandt (1966), Brooks & Dutton (1997), Cheng Tsohsin (1987), Clayton *et al.* (1996), Coates & Bishop (1997), Cranbrook (1984), Delacour (1947), Dickinson (1989a), Dickinson, Kennedy & Parkes (1991), Dickinson, Kennedy, Read & Rozendaal (1989), Good & Wong (1989), Grimmett *et al.* (1998), Hale & Kennerley (1994), Hornslov (1996), Inskipp *et al.* (1996), Jepson (1997), Kang & Lee (1991), Kang *et al.* (1991), Kennerley (1991), Kenneth *et al.* (1995), Langham (1980), Lee, P.G. (1984), Lee, P.G. & Kang (1994), Lee, P.L.M. *et al.* (1996), Lekagul & Round (1991), Lever (1987), MacKinnon & Philipps (1993), Mardiatuti (1996), Mardiatuti & Marnata (1996), Mardiatuti & Soehartono (1996), van Marle & Voous (1988), Marshall & Folley (1956), Medway (1966, 1969), Medway & Wells (1976), Mees (1996), Meyer de Schauensee & Ripley (1940), Ng *et al.* (1986), Nguyễn (1992, 1994), Nguyễn & Voisin (1998), Nugroho & Whendate (1996), Oberholser (1912), Ollington & Loh (1996), Osmaston (1906), Pakpahan & Soehartono (1994), Parrott & Andrew (1996), Pitches (1998b), Riley (1927, 1938), Salomonsen (1983), Sankaran (1995a, 1995b, 1998), Sims (1959, 1961), Smythies (1981, 1986), Stresemann (1914b, 1925, 1931a), Thewlis *et al.* (1996), Tikader (1984), Valli & Summers (1990), Wang (1921), Waugh & Hails (1983), Wells (1999), White & Bruce (1986), Wieruszkeski *et al.* (1987), Xian Yaohua & Zhang Huanying (1983).

39. Papuan Swiftlet

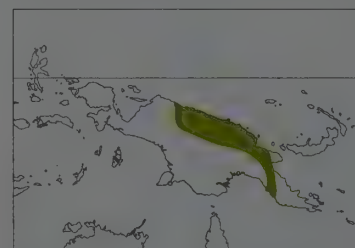
Aerodramus papuensis

French: Salangane papoue **German:** Papuasalangane **Spanish:** Salangana Papú
Other common names: Three-toed Swiftlet, Idenburg (River) Swiftlet

Taxonomy. *Collocalia whiteheadi papuensis* Rand, 1941, Idenburg River, Irian Jaya.

Genus often merged into *Collocalia*. Has been considered conspecific with *A. whiteheadi*, but present species, unique amongst Apodidae, lacks fourth toe. Monotypic.

Distribution. New Guinea: specimens collected from Idenburg R. Snow Mts and Jayapura. Probable sight records from more extensive area of N New Guinea and around Port Moresby in S; first specimen for Papua New Guinea taken from N slopes of Hindenburg Range, Western Province, Apr 1993.



Descriptive notes. 14 cm. Large swiftlet with shallowly forked tail; warm brown, slightly glossy upperparts lacking rump contrast; underparts dark with contrastingly silver-grey throat; densely feathered tarsi; white rami of nape feathers contrast with dark tips. Unique amongst Apodidae in lacking hallux, i.e. has only 3 toes. No information available as to whether or not species is capable of echolocation.

Habitat. Occurs over range of habitats from sea-level to 2400 m. One captured at this upper altitudinal limit was taken at a cave in an area of mossy montane and *Dacrycarpus* forest. May favour gullies in parts of range.

Food and Feeding. Typically feeds at high elevations, though low-level foraging recorded over wetlands. Flocks of 20-30 typical; often with *A. vanikorensis* and *Mearnsia novaeguineae*. In Papua New Guinea one was removed at 06:15 from a net checked at 21:00 previous evening, suggesting crepuscular or even limited nocturnal activity.

Breeding. Not known.

Movements. Resident.

Status and Conservation. Not globally threatened. Thought to be locally common, though lack of definite sightings and scarcity of specimens suggest that this species may actually be rare. Previously considered to be common in Idenburg River area, where flocks of 20-30 individuals were recorded in early 1940's.

Bibliography. Bailey (1992), Beehler *et al.* (1986), Coates (1985), Gregory (1995a, 1995b, 1997), Pratt (1986), Rand (1941), Rand & Gilliard (1967), Rowland, P. (1994), Salomonsen (1962, 1983), Somadikarta (1967, 1975a).

Genus SCHOUTEDENAPUS de Roo, 1968

40. Scarce Swift

Schoutedenapus myoptilus

French: Martinet de Shoa **German:** Maussegler **Spanish:** Vencejo de Shoa
Other common names: Chapin's Swift

Taxonomy. *Cypselus myoptilus* Salvadori, 1888, Let Marefia, Shoa.

Genus previously merged into *Apus*; affinities uncertain. Formerly considered to include *S. schoutedeni* as a race. In past, race *poensis* was considered a race of *Apus unicolor*. Species name sometimes misspelt *myoptilus*. Three subspecies recognized.

Subspecies and Distribution.

S. m. poensis (Alexander, 1903) - Bioko I (Fernando Póo, in Gulf of Guinea).

S. m. chapini (Prigogine, 1957) - E Zaire, Rwanda and SW Uganda.

S. m. myoptilus (Salvadori, 1888) - scattered populations from Ethiopia S to Zimbabwe.



Descriptive notes. 16.5 cm; 22 g. Small swift with long, deeply forked tail appearing needle-thin when closed, bulbous head and thin wings tapering sharply from secondaries; uniform dark grey-brown upperparts with slightly capped appearance; underparts with pale grey throat, mid-brown chest and remainder dark brown, almost chocolate. Race *chapini* has much blacker plumage, while *poensis* is intermediate.

Habitat. Typically in moist highlands, preferably over gorges, waterfalls and evergreen forest. Recorded at 500-2450 m.

Food and Feeding. Flying ants recorded in stomach analysis. Very gregarious; vast single-species flocks, Apr-Aug, in parts of E Zaire. Recorded feeding in large flocks very high over lowland forests, W Kenya, especially in afternoons when poor weather over adjacent highlands may force this lower-altitude feeding. Often forages very low during dry weather, believed to be feeding largely on termites.

Breeding. Egg-laying believed to occur between Sept and Dec in Zimbabwe; analysis of sexual organs suggests breeding occurs in Zaire around Feb and also Sept, while specimens with enlarged gonads were taken in mid-May on Mt Moroto, Uganda, in early Jul at Kapenguria, Kenya, and in early Sept on Mt Mlanje, Malawi; *poensis* may breed in N summer as birds with nearly completed primary moult recorded late Dec to early Jan. Nest not recorded, due to apparent inaccessibility of sites, which are thought to be on cliff-faces or rock clefts, or close to waterfalls on high mountains.

Movements. Typically resident, though regional movements recorded. In E Zaire around Kamituga and Tubangwa, rare Oct-Dec and common Jul-Sept, though resident in adjacent highlands. Present as summer breeder only in mountainous areas of Zimbabwe, close to border with Mozambique. Recent records from Taita Hills, in SE Kenya, where species does not breed, indicate some wandering.

Status and Conservation. Not globally threatened. Varies considerably in status throughout range. Abundant in some wet mountainous areas of E Africa, but elsewhere far more local. Scattered distribution, with numerous seemingly extralimital records, suggest range may be wider than currently thought. Reported from several protected areas, e.g. Kibale Forest National Park (Uganda), Kibira National Park (Burundi) and Nyika National Park (Malawi).

Bibliography. Benson (1952), Benson & Benson (1977), Benson *et al.* (1971), Brooke (1968, 1971a, 1971d, 1971i), Dillingham (1958), Dowsett (1977a, 1990), Dowsett & Dowsett-Lemaire (1978b, 1993), Dowsett & Forbes-Watson

(1993), Dowsett-Lemaire (1989), Duckworth *et al.* (1992), Fry *et al.* (1988), Ginn *et al.* (1989), Grant & Mackworth-Praed (1937), Harrison *et al.* (1997), Lewis & Pomeroy (1989), Lippens & Wille (1976), Mackworth-Praed & Grant (1957, 1962, 1970), Maclean (1993), Mann (1976), Newman *et al.* (1992), Nikolaus (1987), Pérez del Val (1996), Pérez del Val *et al.* (1994), Pinto (1983), Prigogine (1960, 1966), de Roo (1968), Scott (1979), Short *et al.* (1990), Snow (1978), White (1965), Williams (1980), Zimmerman, D.A. *et al.* (1996).

41. Schouteden's Swift

Schoutedenapus schoutedeni

French: Martinet de Schouteden **German:** Schoutedensegler **Spanish:** Vencejo del Congo
Other common names: Congo Swift

Taxonomy. *Apus schoutedeni* Prigogine, 1960, Butokolo, Zaire.

Genus previously merged into *Apus*; affinities uncertain. Formerly considered a race of *S. myoptilus*. Monotypic.

Distribution. E Zaire, where collected from Mubandakika, Butokolo, Bionga and Kamituga.



Descriptive notes. 16.5 cm. Small swift with structure similar to that of *S. myoptilus*; long, thin, deeply forked tail, though this probably averages shorter than in *S. myoptilus*, with less emargination in shorter outer rectrix; bulbous head and wings tapering sharply from secondaries; uniformly black-brown plumage including throat.

Habitat. Presumed to be a highland species, mainly because was collected from Butokolo at 1470 m.

Food and Feeding. Nothing known; presumably similar to congener.

Breeding. Female collected in Feb had enlarged oocytes; two specimens from Oct did not have enlarged gonads.

Movements. Not known.

Status and Conservation. **VULNERABLE.** Restricted-range species: present in Eastern Zaire Lowlands EBA. Still known from only five specimens. Habitat within species' range thought still to be in reasonably good condition; however, deterioration or loss of habitat may be greatest threat, although preferences of species still remain essentially unknown. Much research and survey work required in order to establish current status and conservation requirements.

Bibliography. Brooke (1971a, 1971d, 1971i), Collar & Andrew (1988), Collar & Stuart (1985, 1988a), Collar *et al.* (1994), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Fry *et al.* (1988), Hall & Moerau (1962), Lippens & Wille (1976), Mackworth-Praed & Grant (1970), Prigogine (1960, 1971, 1978), de Roo (1968), Schouteden (1968), Snow (1978), Stattersfield *et al.* (1998), White (1965), Wilson & Catsis (1990).



Tribe CHAETURINI

Genus *MEARNSIA* Ridgway, 1911

42. Philippine Spinetail

Mearnsia picina

French: Martinet des Philippines **German:** Philippinensegler **Spanish:** Vencejo Filipino
Other common names: Philippine Needletail, Philippine Spine-tailed Swift/Needletail

Taxonomy. *Chaetura picina* Tweeddale, 1879, Zamboanga, Mindanao. Previously placed in *Chaetura*. Monotypic.

Distribution. SC & S Philippines on Leyte, Negros, Cebu, Biliran, Samar and Mindanao.



Descriptive notes. 14 cm. Large spinetail with very long wings hooked in outer wing, bulging midwing and pinched in at body; large head and relatively short, square tail, appearing more rounded when spread, rectrix spines extending up to 1.2 mm beyond web. Very black plumage broken only by small, but highly distinct, white throat-patch and equally striking white patches on underwing-coverts, last feature unique in Apodiformes.

Habitat. Apparently a forest species.

Food and Feeding. Usually seen at high elevations alone or in small groups.

Breeding. Not known.

Movements. Resident.

Status and Conservation. Not globally threatened. Restricted-range species: present in Negros and Panay EBA, Cebu EBA (extinct), Mindanao and the Eastern Visayas EBA and Sulu Archipelago EBA. Believed to be uncommon throughout range. Recorded in low numbers during 1991 survey of Negros. Occurs in Mount Canlaon National Park, Negros.

Bibliography. Brooks & Dutton (1997), Brooks, Evans *et al.* (1992), Brooks, Magsalay *et al.* (1995), Delacour & Mayr (1946), Dickinson *et al.* (1991), Evans, Dutton & Brooks (1993), Hachisuka (1934), Inskipp *et al.* (1996), Lambert (1993), McGregor (1909-1910, 1921), Rand (1951a), Stattersfield *et al.* (1998).

43. Papuan Spinetail

Mearnsia novaeguineae

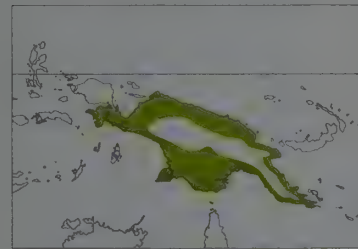
French: Martinet papou **German:** Papuasegler **Spanish:** Vencejo Papú
Other common names: Papuan/New Guinea Spinetail/Spinetailed Swift/Needletail, Grey-bellied Needletail

Taxonomy. *Chaetura novaeguineae* D'Alberty and Salvadori, 1879, Fly River, New Guinea. Previously placed in *Chaetura*, and earlier in monospecific genus *Papuanapus*. Proposed race *mamberana*, known from mouth of Mamberano R, nowadays included in *buergersi*. Two subspecies currently recognized.

Subspecies and Distribution.

M. n. buergersi (Reichenow, 1917) - N New Guinea.

M. n. novaeguineae (D'Alberty & Salvadori, 1879) - S & SE New Guinea.



Descriptive notes. 11.5 cm. Small spinetail with large head, short square tail appearing rounded when spread, rectrix spines up to 1 mm beyond web, and distinct wing shape which is hooked in outer wing, has bulging midwing and then pinches in at body. Very glossy plumage, black with green sheen above; black tail and undertail-coverts; grey-brown throat with remainder of underparts strikingly white. Race *buergersi* has paler throat and relatively even whiter underparts.

Habitat. Lowland species not recorded over 550 m. Found primarily over forested areas on coast and in interior; can be recorded around

settlements. In lowland rainforest zone of Papua New Guinea recorded over forest edge and non-forest.

Food and Feeding. Typically forages in pairs or small flocks, groups over 40 not unknown. Often associates with swiftlets. Very active in crepuscular period. Feeds at low elevations, at tree height and below, particularly around dead trees. May take insects directly from foliage.

Breeding. Breeds in second half of dry season in Trans-Vanapa, Central Province. Nests in hollows in trees; recorded entering hollow trunk of burnt sago palm, 7 m high; has been recorded collecting fibres from dry palms, which it presumably uses in nest construction.

Movements. Resident; may show some local dispersal.

Status and Conservation. Not globally threatened. Frequency varies locally from scarce to abundant in suitable habitat; locally common around Kiunga, on upper Fly R. Record in 1992 of 10 birds in W Vogelkop region, where species previously unknown may suggest dispersal or perhaps some sort of range expansion.

Bibliography. Anon. (1994a), Beehler, Pratt & Zimmerman (1986), Beehler, Sengo *et al.* (1995), Burrows (1993), Coates (1977, 1985), Finch (1981), Gregory (1995a, 1995b, 1996), Hicks (1988c, 1989), Mayr & Rand (1937), Murray (1988), Rand & Gilliard (1967), Ripley (1964a).

Genus *ZOONAVENA* Mathews, 1918

44. Madagascar Spinetail

Zoonavena grandidieri

French: Martinet de Grandidier **German:** Malegassensegler **Spanish:** Vencejo Malgache
Other common names: Madagascar Spine-tailed Swift, Malagasy Spinetail/Needletail

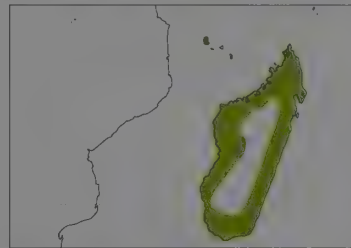
Taxonomy. *Chaetura grandidieri* J. Verreaux, 1867, Mandrisis, eastern Madagascar.

Previously placed in *Chaetura*. Two subspecies recognized.

Subspecies and Distribution.

Z. g. grandidieri (J. Verreaux, 1867) - Madagascar.

Z. g. mariae (Benson, 1960) - Grand Comoro (Ngazidja) in Comoro Is.



Descriptive notes. 12 cm. Small spinetail with typical wing shape, hooked in outer wing and bulging in midwing; square tail appears slightly cleft in some views and rounded when spread, rectrix spines extending up to 3 mm and 1.5 mm respectively in those male and females measured. Black-brown upperparts broken by heavy streaked white rump; rather uniform pale grey-brown underbody. Race *mariae* averages shorter-winged and has darker rump.

Habitat. Essentially a forest species. In Madagascar occurs over wide range of habitats, particularly with very large trees, but also over paddies, mainly in lowlands to 1000 m though

found to 1400 m in Marojejy reserve. On Grand Comoro infrequent away from forest, at 400-1750 m, less often at lower altitudes right down to sea-level.

Food and Feeding. Insects. Forages low over canopy or between trees close to ground, alone or in pairs or small flocks, up to 15 recorded together.

Breeding. Season thought to be Apr-Jan, though birds with enlarged gonads have been collected in Jul, Aug, Sept, Oct, Jan, Mar and May, indicating year-round breeding; aerial copulation reported mid-Sept. Nests in various holes such as tree hollows, rock niches and wells; nest composed of various vegetable matter including twigs.

Movements. Resident.

Status and Conservation. Not globally threatened. Rather common, especially in moister E areas of Madagascar. Occurs in Perinet Special Reserve, c. 150 km E of Antananarivo. Widespread in suitable habitat on Grand Comoro, but numbers generally low, and rare at some sites, such as La Grille.

Bibliography. Appert (1972, 1996), Benson (1960), Benson *et al.* (1976-1977), Brooke (1971), Dee (1986), Delacour (1930), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Garino (1996), Langrand (1994, 1995), Lavauden (1937), Louette (1988a), Louette & Stevens (1992), Louette *et al.* (1988), Milon *et al.* (1973), Morris & Hawkins (1998), Rand (1936), Safford & Duckworth (1990), Sinclair & Langrand (1998), Snow (1978), Stevens, Herremans & Louette (1992), Stevens, Louette *et al.* (1995), Thompson & Buisson (1988), Thorstorn & Watson (1997).

45. Sao Tome Spinetail

Zoonavena thomensis

French: Martinet de Sao Tomé **German:** Sao-Tomé-Segler **Spanish:** Vencejo de Santo Tomé
Other common names: Sao Tome Spine-tailed Swift

Taxonomy. *Chaetura thomensis* Hartert, 1900, São Tomé.

Previously placed in *Chaetura*. In past, considered possibly conspecific with *Rhaphidura sabini*, but this view now unanimously rejected. Monotypic.

Distribution. São Tomé and Príncipe, in Gulf of Guinea.



Descriptive notes. 10 cm; c. 8 g. A tiny spinetail with typical spinetail wing shape, hooked in outer wing with bulging midwing, and square tail, appearing rounded when spread, rectrix spines 1.2-2.5 mm beyond web. Black-brown upperparts broken by broad pale rump-band; brown throat indistinctly separated from heavily streaked off-white underparts.

Habitat. Essentially a forest species, primary or secondary, but also over adjacent cultivated areas and plantations. Found from lowland to 1500 m on São Tomé, mainly at 200-800 m in E and between sea-level and 400 m in W, and to 500 m on Príncipe. Apparently avoids *Apus*

affinis, which occupies low elevations, in E São Tomé, but forms mixed flocks with this species on Príncipe and nearby Prince I.

Food and Feeding. Insects, including tiny beetles. Forages in groups of 8-10, circling trees and also performing "figures of eight" 5-10 m above ground.

Breeding. Inferred egg-laying in early Aug and late Oct on São Tomé, and in Sept on Príncipe. Solitary nester. Open, cupped, nest structure, 15-25 mm long, stuck to vertical side of hollow tree, e.g. silk-cotton (*Ceiba pentandra*), 3 m above floor or lower, 20-40 cm above ground when among buttress roots; old nests found in hollows presumed to be previous season's nest of active pair. Clutch 2-3, sometimes 4.

Movements. Resident.

Status and Conservation. Not globally threatened. Restricted-range species: present in São Tomé EBA and Príncipe EBA. Common on both islands.

On following pages: 46. White-rumped Spinetail (*Zoonavena sylvatica*); 47. Mottled Spinetail (*Telecanthura ussheri*); 48. Black Spinetail (*Telecanthura melanopygia*); 49. Silver-rumped Spinetail (*Rhaphidura leucopygialis*); 50. Sabine's Spinetail (*Rhaphidura sabini*); 51. Cassin's Spinetail (*Neorapapap cassinii*); 52. Böhm's Spinetail (*Neorapapap boehmi*); 53. White-throated Needletail (*Hirundapus caudacutus*); 54. Silver-backed Needletail (*Hirundapus cochinchinensis*); 55. Brown-backed Needletail (*Hirundapus giganteus*); 56. Purple Needletail (*Hirundapus celebensis*).

Bibliography. Amadon (1953), Atkinson, Dutton *et al.* (1994), Atkinson, Peet & Alexander (1991), Christy (1998), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Frade (1958), Fry *et al.* (1988), Garino (1996), Jones & Tye (1988), Mackworth-Præd & Grant (1970), de Naurois (1985, 1994b), Sargeant (1992a, 1994c), Snow (1950, 1978), Stattersfield *et al.* (1998).

46. White-rumped Spinetail

Zoonavena sylvatica

French: Martinet indien **German:** Hindusegler **Spanish:** Vencejo Indio
Other common names: Indian White-rumped Spinetail/Spine-tailed Swift, White-rumped Needletail

Taxonomy. *Acanthylis sylvatica* Tickell, 1846, central India. Previously placed in *Chaetura*. Monotypic.

Distribution. S of Himalayas from NC India (N Uttar Pradesh) and Nepal S through E & EC India, and E to W Myanmar, where status uncertain; also S through Western Ghats to S Kerala.



Descriptive notes. 11 cm; 13 g. Small spinetail with short square tail, rounded when spread, relatively large head and distinctive wing shape, hooked outer wing, bulging midwing and pinched in at body; rectrix spines up to 4 mm beyond webs. Blackish upperparts broken by white rump-band which is contiguous with white underparts that contrast with indistinct grey throat.

Habitat. In Himalayas found to 1770 m, though generally at lower altitudes over variety of forest types, including plantations.

Food and Feeding. Mainly Coleoptera and Hemiptera. Usually forages in small groups,

though up to 50 have been recorded together, over forested and adjacent habitats.

Breeding. Season mainly Mar-Apr, though recorded Feb-May, Western Ghats. Believed to be a solitary breeder; multiple nests at some sites suggest new nests are used in traditional sites. Nests are depressions lined with dry leaves and straw, in debris at base of hollow trunks in old humid forest trees. Clutch 3-4, occasionally 5.

Movements. Largely resident, but with some dispersal, which appears to be without pattern.

Status and Conservation. Not globally threatened. Generally rather local and uncommon, but sometimes abundant; groups of up to 50 individuals occasionally recorded, but numbers are normally much lower. In Nepal, local and uncommon, though seen with some regularity at Chitwan National Park. Occurs in several protected areas in India, e.g. Corbett, Indira Gandhi and Periyar National Parks.

Bibliography. Ali (1935-1937), Ali & Grubb (1976), Ali & Ripley (1983), Anon. (1994b), Daniels (1997), Grimmett *et al.* (1998), Inskipp, C. & Inskipp (1991), Inskipp, T. *et al.* (1996), Javed & Rahmani (1998), Kannan (1998), Ripley (1982), Stewart (1913), Sugathan & Varghese (1996).

Genus *TELECANTHURA* Mathews, 1918

47. Mottled Spinetail

Telecanthura ussheri

French: Martinet d'Ussher **German:** Baobabssegler **Spanish:** Vencejo de Baobab
Other common names: Ussher's/Mottled-throated Spinetail/Spinetailed Swift

Taxonomy. *Chetura ussheri* Sharpe, 1870, Ghana.

Genus formerly merged into *Chaetura*, or occasionally *Rhaphidura*. It has been suggested that present species may be better treated as two due to differences in plumage, structure and habitat, though precise situation of dividing line unclear. Proposed race *marwitzi* of Wemberere steppe, Tanzania, known only from type, and believed to represent aberrant individual of race *stictilaema*. Four subspecies currently recognized.

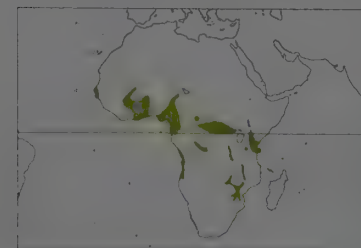
Subspecies and Distribution.

T. u. ussheri (Sharpe, 1870) - broken range from Senegambia to Nigeria.

T. u. sharpei (Neumann, 1908) - Cameroon to Gabon, and Zaire E to Uganda.

T. u. stictilaema (Reichenow, 1879) - CE Africa, and recently also Zanzibar and Pemba I.

T. u. benguellensis (Neumann, 1908) - W Angola and SE Africa.



Descriptive notes. 14 cm; male 33 g, female 34-5 g. Medium-sized spinetail with typical spinetail "butter-knife" wing shape, with hooked outer wing, bulging inner primaries and outer secondaries and pinched in at body; prominent tail, appearing rounded when spread and square when closed, rectrix spines 2-4 mm beyond web; large head; pale-mottled throat and white rump and ventral area on otherwise black-brown upperparts and underparts. Race *sharpei* is blackest subspecies, with browner throat-patch and longer tail than nominate; *stictilaema* blacker than nominate with shorter wings and longer tail; *benguellensis* is brown-

est race, with browner throat and greyer underparts, white ventral patch less contrasting.

Habitat. A lowland species over much of range, though recorded to 2200 m in E Africa and 900 m in Zambia. Found over variety of habitats, including gallery forest and clearings in evergreen forest, generally avoiding human habitation. Preferred habitat appears to be dry deciduous woodland dominated by baobabs (*Adansonia digitata*). Shows preference for coastal zone in Senegal, parts of E Africa and Angola. In Ivory Coast prefers *Borassus* palm savanna. Racial preferences in habitat: nominate form in deciduous forest and occasionally in upper Guinea forest types; *sharpei* in evergreen forest; *stictilaema* in dry deciduous and less frequently evergreen forest; *benguellensis* more often in woodland than forest.

Food and Feeding. Winged ants and small numbers of flies, termites and Hymenoptera. Highly mobile when foraging and often seen only fleetingly. Typically in pairs or small groups, though an exceptional flock of 100 recorded. Associates with other swifts and hirundines.

Breeding. Breeds Transvaal Apr-May; enlarged gonads Zaire Jan and Jul-Aug, Cameroon Feb, Kenya Feb and Apr, Uganda Mar and Sept; copulation Tanzania Dec; laying Cameroon Jan-Mar, Babonde, Zaire, Jun; nestlings Ghana Mar, Zaire Apr-May and Aug-Sept, Cameroon May-Jun and Oct. Solitary. Nests in hollow trees, especially baobabs; also in chimney stacks, on walls or under beams of houses; uses new nest in each breeding season as up to 4-5 old nests noted in a hollow. Salivary glands enlarged in both sexes, suggesting both build; strong bracket-shaped nest of dry twigs typically 2 cm long and other vegetable matter, agglutinated with saliva, with curtain of twigs hanging below structure; whole structure measures 75-80 mm at point of attachment. Copulates in flight. 4 eggs.

Movements. Resident throughout much of range, yet some seasonal movements recorded. Occurs in SW Mt Kenya during Sept-Jan, and absent from Mampong, Ghana, Sept-Jan, where frequent Feb-Jun and common Mar-May during breeding season.

Status and Conservation. Not globally threatened. Status varies throughout range. Most abundant in parts of E & C Africa, rarest in limited S African range, where it is thought that protection of baobab habitats will give it a secure future. In 1984, South Africa was believed to hold fewer than 50 pairs, though perhaps as many as 300 individuals; classified as Red Data Species for the country; recently, regularly recorded in N sector of Kruger National Park. Also believed to be rarest Liberian spinetail, though status there uncertain; only handful of records from Sierra Leone. Considered uncommon throughout Kenyan range but can be recorded daily in reasonable numbers, in summer at least, along coastal strip. Occurs in a number of protected areas across its sizeable range, e.g. Niokola Koba National Park (Senegal) and Mikumi National Park (Tanzania).

Bibliography. Anon. (1998b), Archer & Iles (1998), Archer & Turner (1993), Ash & Miskell (1998), Barlow *et al.* (1997), Benson (1977), Benson & Benson (1977), Benson & Winterbottom (1977), Benson *et al.* (1971), Brooke (1968, 1971c, 1971e, 1971i, 1984), Chantler & Driessens (1995b), Chapin (1939), Cheke & Walsh (1996), Clancey (1968), Colston & Curry-Lindahl (1986), Dowsett (1989a), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Elgood *et al.* (1994), Field (1998), Friedmann (1930), Fry *et al.* (1988), Garino (1996), Gatter (1988, 1997), Ginn *et al.* (1989), Gore (1990), Grant & Mackworth-Præd (1937), Grimes (1972, 1987), Harrison *et al.* (1997), Heigham & Ryder (1981), Lewis & Pomeroy (1989), Lippens & Wille (1976), Louette (1981), Mackworth-Præd & Grant (1937, 1957, 1962, 1970), Maclean (1993), Moreau & Moreau (1937), Newman *et al.* (1992), Pinto (1983), Serie *et al.* (1977), Short *et al.* (1990), Snow (1978), Williams (1980), Zimmerman, D.A. *et al.* (1996).

48. Black Spinetail

Telecanthura melanopygia

French: Martinet de Chapin **German:** Iturisegler **Spanish:** Vencejo del Ituri
Other common names: Chapin's Spinetail, Ituri (Mottled-throated) Spinetail/Spinetailed Swift

Taxonomy. *Chaetura melanopygia* Chapin, 1915, Avakubi, Ituri District, Zaire.

Genus formerly merged into *Chaetura*, or occasionally *Rhaphidura*. Monotypic.

Distribution. Sierra Leone to S Ghana, Nigeria, Cameroon and Gabon; also SW Central African Republic, NE Zaire and NE Angola.



Descriptive notes. 15 cm; 52 g. Large, slender spinetail with long wings, typical hooked outer primaries, bulging inner primaries and outer secondaries, pinched in at body; prominent tail appears rounded when spread and square when closed; rectrix spines up to 6 mm beyond web. Dark black-brown, especially above, broken only by underwing contrast and paler mottling on throat.

Habitat. Rainforest zone over a variety of habitats, including primary and secondary forest, plantations and rocky outcrops.

Food and Feeding. Winged ants reported from 1 stomach. Generally a low-elevation feeder

that freely associates with other swifts and also Square-tailed Saw-wing (*Psilidoprocne nitens*). Seen singly or in groups of up to 12.

Breeding. Largely unknown. Enlarged gonads in Ghana in Feb, and Zaire in Oct; entering tree hollows in Liberia late Dec to mid-Mar, where aerial copulation mid-Dec and late Jan. Possibly nests in crags rising above forest.

Movements. Generally considered resident. Some authors have suggested that this may be an afrotropical migrant, although it has been speculated that it may just wander considerable distances over suitable habitat. Migrates from Liberia in rainy season.

Status and Conservation. Not globally threatened. Locally uncommon to rare throughout, but believed to occur more widely than present knowledge indicates, and certainly overlooked. Some evidence that it occurs in higher densities in Liberia since fragmentation of habitat. Report of 60 birds at 1 site in SW Ghana in Sept 1989. Occurs in Gola Forest Reserves (Sierra Leone), Tai Forest National Park (Ivory Coast) and Korup National Park (Cameroon).

Bibliography. Allport *et al.* (1989), Anon. (1998b), Brooke (1971i), Brosset & Éard (1986), Carroll (1988), Chapin (1939), Cheke & Walsh (1996), Colston & Curry-Lindahl (1986), Deme & Fishpool (1991, 1994), Dowsett & Dowsett-Lemaire (1993, 1997), Dowsett & Forbes-Watson (1993), Elgood *et al.* (1994), Field (1998), Fry *et al.* (1988), Garino (1996), Gatter (1988, 1997), Green & Carroll (1991), Green & Rodewald (1996), Grimes (1987), Heim de Balsac & Brosset (1964), Lippens & Wille (1976), Lockwood *et al.* (1980), Louette (1981), Mackworth-Præd & Grant (1970), Pinto (1983), Rodewald *et al.* (1994), Snow (1978), Thiollay (1985), Traylor (1963).

Genus *RHAPHIDURA* Oates, 1883

49. Silver-rumped Spinetail

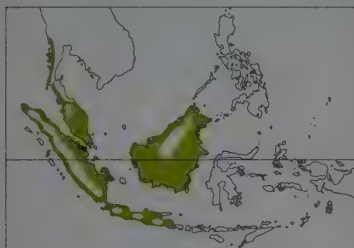
Rhaphidura leucopygialis

French: Martinet leucopyge **German:** Silberbüzelssegler **Spanish:** Vencejo Cutiplata
Other common names: Silver-rumped (Spine-tailed) Swift, Silver-rumped Needletail, White-rumped Spinetail(!)

Taxonomy. *Acanthylis leucopygialis* Blyth, 1849, Penang.

Genus formerly merged into *Chaetura*. Monotypic.

Distribution. S Myanmar to Malay Peninsula, Sumatra, and Bangka I, Borneo and Java.



Descriptive notes. 11 cm. Small spinetail with typical wing shape, hooked outer wing, bulging midwing, sharply pinched in at body; protruding head and square tail, appearing rounded when spread, rectrix spines up to 4 mm beyond web. Very black plumage with sharply contrasting white rump and uppertail-coverts, actually grey-tinged with shaft streaking at close range.

Habitat. Mainly lowlands to 600 m in Sumatra, 1500 m in Java and 1250 m in Malay Peninsula. Occurs over forests, primary and secondary growth, and plantations often close to water, including estuarine habitats where more regular than over fresh water in one Sarawak study.

Infrequent near human settlements.

Food and Feeding. Forages around clearings or rock outcrops in forest. Malaysian study noted larger numbers feeding over forested areas and mainly in higher strata, over 30 m, though lower than other high-elevation group feeders - *Hirundapus*, *Apus pacificus* and *A. affinis*. Mean foraging height lower over forested areas than elsewhere (40 m as compared to 43 m) and 31% of foraging occurs within 10 m of vegetation. Especially active in evening. Not often seen with other species and rarely in groups of more than 6.

Breeding. Little studied. During May-Jun several birds were thought to be nesting in a hollow tree in Borneo, possibly colonially. Nests in hollow trees.

Movements. Resident.

Status and Conservation. Not globally threatened. Locally common in suitable habitat, though uncommon in Java. During major study of aerial feeding in W Malaysia, this was least frequently encountered of all identified swift species. Occurs in many protected areas, e.g. Taman Negara National Park (Malaysia), Way Kambas National Park (Sumatra), Gunung Mulu and Bako National Parks (Sarawak), and Khao Nor Chuchi Non-hunting Area (Thailand).

Bibliography. Davison (1995, 1997a, 1997b), Duckworth & Kelsch (1988), Inskipp *et al.* (1996), Lekagui & Round (1991), MacKinnon (1988), MacKinnon & Phillips (1993), van Marle & Voous (1988), Medway & Wells (1976), Meyer de Schauensee & Ripley (1940), Nash & Nash (1988), Parrott & Andrew (1996), Rajathurai (1996), Riley (1938), Smith (1977), Smythies (1981, 1986), Vowles & Vowles (1984), Waugh & Hails (1983), Wells (1999), Wilkinson *et al.* (1991).

50. Sabine's Spinetail

Rhaphidura sabini

French: Martinet de Sabine

German: Sumpfsegler

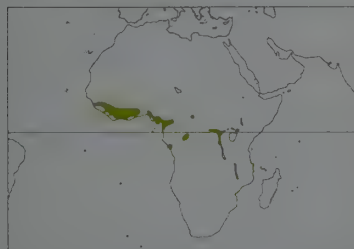
Spanish: Vencejo de Sabine

Other common names: Sabine's Spine-tailed Swift

Taxonomy. *Chaetura Sabini* J. E. Gray, 1829, Sierra Leone.

Genus formerly merged into *Chaetura*. Has been considered possibly conspecific with *Zoonavena thomensis*, but this view has not gained support and is contradicted by considerable dissimilarities. Birds of R Ogowe (Gabon) previously recognized as race *ogowensis*, by virtue of alleged smaller size. Monotypic.

Distribution. Broken range from S Guinea to NW Gabon and coastal & C Congo, then through NW & E Zaire and S Central African Republic to W Uganda; isolated population in W Kenya.



Descriptive notes. 11-5 cm; average male 20 g, female 19 g. Small, elegant spinetail with relatively large head and distinctive wing shape, hooked outer wing, bulging midwing and pinched in at body; short square tail, appearing rounded when spread, rectrix spines up to 4 mm beyond web. Blackish upperparts broken by broad white band on rump and uppertail-coverts, contiguous with white underparts which contrast strongly with black upper breast and throat; white areas of plumage faintly dark-streaked.

Habitat. A rainforest species typically found at 700-1700 m, though also in lowlands, around

forest edges and clearings but also over nearby grasslands and even mangroves. Often close to water; freshwater riverine swamps with very large solitary trees and low vegetation thought to be optimum habitat in Liberia, along with border zone between forest and montane savannas.

Food and Feeding. Flying and wingless ants, flies, small beetles, and insects resembling mosquitoes recorded. Typically seen close to ground, but sometimes at great height over canopy.

Breeding. Probably breeding Liberia Mar, Apr and Sept; enlarged gonads Liberia Mar-Apr, Cameroon May, Kenya and Zaire Jun; egg-laying Cameroon Mar and probably May; nestlings Kenya Jan or Feb, Zaire Jun and Aug. Nests singly or 2 pairs together in tree hollows or niches among large tree roots; probably within suitable man-made structures on occasions. Small half-cupped nest of twigs attached to vertical surface. Clutch 2-3.

Movements. Believed resident throughout much of range, though data from Liberia suggest it is a partial migrant there.

Status and Conservation. Not globally threatened. Fairly common to common. Least abundant in tiny W Kenyan range, where perhaps some decline in 20th century, as indicated by paucity of recent records. Current density in Liberia perhaps greater than it was before forest fragmentation, as species will occupy secondary habitats. Not uncommon in Ghana, where is commonest spinetail in Bia National Park. In Sierra Leone, common in all of the larger forests. In Cameroon, occurs on Mt Cameroon and Mt Kupé; also found on Mt Nimba, Liberia, and in Tai Forest National Park.

Bibliography. Allport *et al.* (1989), Bannerman (1933), Bates (1911, 1930), Britton (1970), Brooke (1971c, 1971i), Carroll (1988), Cheke & Walsh (1996), Christy & Clarke (1994), Colston & Curry-Lindahl (1986), Demey & Fishpool (1991, 1994), Dowsett (1989b), Dowsett & Dowsett-Lemaire (1991, 1993, 1997), Dowsett & Forbes-Watson (1993), Elgood *et al.* (1994), Field (1974, 1998), Fry *et al.* (1988), Garino (1996), Gatter (1988, 1997), Germain & Cornet (1994), Gore (1994), Green & Carroll (1991), Grimes (1987), Halleux (1994), Lewis & Pomeroy (1989), Lippens & Wille (1976), Louette (1981), Mackworth-Præd & Grant (1957, 1970), Mann (1976), Pérez del Val (1996), Pinto (1983), Rodewald *et al.* (1994), Serle *et al.* (1977), Short *et al.* (1990), Snow (1978), Thiollay (1985), Traylor (1963), Williams (1960, 1980), Wilson (1990), Zimmerman, D.A. *et al.* (1996).

Genus NEAFRAPUS Mathews, 1918

51. Cassin's Spinetail

Neafrapus cassini

French: Martinet de Cassin

German: Cassinsegler

Spanish: Vencejo de Cassin

Other common names: Cassin's Spine-tailed Swift

Taxonomy. *Chaetura cassini* P. L. Selater, 1863, Gabon.

Genus formerly merged with *Chaetura* or *Mearnsia*. Race *brevicauda* of Bipindi (Cameroon) has been recognized but consistent geographical variation is lacking in this species. Monotypic.

Distribution. E Sierra Leone and Liberia to Ghana, and SW Nigeria to Cabinda (extreme N Angola); Bioko I; also extreme E Congo through N Zaire and SW Central African Republic to W Uganda.



Descriptive notes. 15 cm; 39.5 g. Large spinetail with remarkably short, square tail with rectrix spines up to 6 mm beyond webs, large bulging head, long-winged appearance and typical spinetail wing shape, with especially bulging secondaries and hooked outer wing. Black-brown upperparts broken by narrow white rump band; grey throat and black flanks, especially noticeable on rear flanks, contrast with lightly streaked white underparts.

Habitat. Restricted to rainforest zone, where forest lakes seem to be preferred habitat to feed over. Adjoining secondary growth and plantations sometimes visited. Original habitat

intraforest riverine swamps with large trees, but increasingly occupies forest edge and clearings near water.

Food and Feeding. Flying ants and smaller numbers of termites and small beetles recorded; also 200 leafhoppers (Cicadellidae) and 100 termites in 1 stomach. During day often feeds at great height, while crepuscular feeding usually at low level. Often with sympatric spinetails, especially *Rhaphidura sabini*. Gregarious, up to 40 recorded together, though smaller flocks more typical.

Breeding. Although not proven, considerable circumstantial evidence points to nesting in hollow trees; no nest found to date. Enlarged gonads on Bioko Jul, in Zaire Jul, Sept and Nov; flights and tree hollow visits Liberia Feb-Apr; postulated laying dates in Zaire Apr and Jul, Gabon c. Aug-Sept; watched leaving hollow tree with feathers belonging to this species at base, with eggshell, Avakubi, Zaire, Apr; believed to be feeding young in hollow stump Zaire, Jul, and among cavities in dead trees Gabon, Oct. No further information available.

Movements. Resident throughout much of range, but Liberian data suggest some migration with absence during rains in SE. May be transequatorial migrant.

Status and Conservation. Not globally threatened. Uncommon throughout most of range. In Liberia, where uncommon, found in all studied forests, usually in groups of 5 birds or fewer though up to 15 individuals sometimes recorded. Uncommon in Ghana, where not recorded until 1960's, though uncertain whether this reflects range expansion or that species was previously overlooked; recorded in Bia National Park and Subri River Forest Reserve. In Sierra Leone, known only from environs of Gola Forest, where only recently found to occur. Occurs in Tai Forest National Park.

Bibliography. Amadon (1953), Bannerman (1953), Brooke (1971c, 1971i), Chapin (1939), Cheke & Walsh (1996), Christy & Clarke (1994), Colston & Curry-Lindahl (1986), Dowsett & Dowsett-Lemaire (1991, 1993), Dowsett & Forbes-Watson (1993), Eiseutraut (1973), Elgood *et al.* (1994), Field (1998), Fry *et al.* (1988), Garino (1996), Gatter (1997), Green & Carroll (1991), Grimes (1987), Keith (1968), Lippens & Wille (1976), Louette (1981), Mackworth-Præd & Grant (1970), Pérez del Val (1996), Pérez del Val *et al.* (1997), Pinto (1983), Serle *et al.* (1977), Short *et al.* (1990), Snow (1978), Sutton (1965), Traylor (1963), Wells (1968).

52. Böhm's Spinetail

Neafrapus boehmi

French: Martinet de Böhm

German: Fledermaussegler

Spanish: Vencejo de Böhm

Other common names: Böhm's Spine-tailed Swift, Bat-like Spinetail

Taxonomy. *Chaetura Böhm* Schallow, 1882, Tanzania.

Genus formerly merged with *Chaetura* or *Mearnsia*. Intergrades between nominate race and *sheppardii* occur in upper Zambezi Valley. Two subspecies normally recognized.

Subspecies and Distribution.

N. b. boehmi (Schallow, 1882) - W & CE Angola, S Zaire, W & N Zambia and W Tanzania.

N. b. sheppardii (Roberts, 1922) - SE Kenya and E Tanzania; E & SE Zambia, N & E Zimbabwe, Mozambique and NE South Africa.



Descriptive notes. 10 cm; 14.5 g. A small spinetail with a quite remarkable appearance: large head, very short, square tail, rectrix spines up to 3.5 mm beyond webs, and long wings with hooked outer wing and deeply bulging midwing, pinched in sharply at body. Black-brown upperparts broken by broad white rump, broader than in *N. cassini*; underparts white with contrasting grey throat and black flanks. Slightly smaller race *sheppardii* has paler lower throat and more obvious shafting on underparts and white fringing to fresh rectrices.

Habitat. A lowland species, mainly below 600 m but recorded at 900 m in Zimbabwe and 1300

m in Tanzania. Frequents range of primary savanna woodlands, typically quite open, arid and deciduous, with baobab (*Adansonia digitata*), miombo and *Cryptosepalum*, as well as edges and clearings in denser evergreen forest, both gallery and larger expanses.

Food and Feeding. Flies, beetles and ants recorded. Highly gregarious, associating with various species of saw-wing swallow (*Psittidoprocne*), *Telecanthura ussheri* and *Cypsiurus parvus*. Forages close to large trees. Noted in groups of 2-6 at Kariba, Zimbabwe, with Lesser Striped Swallows (*Hirundo abyssinica*), Wire-tailed Swallows (*H. smithii*) and *C. parvus* in lowest of 3 feeding levels,

below 20 m. This stratification apparent only when several species present; fed at other levels when alone or with just 1 other species.

Breeding. Egg-laying Kenya Jan or Feb, Tanzania Apr, Kasai, Zaire, Oct, Zambia Sept-Oct and Jan, South Africa Apr; newly fledged young Angola Feb, Zimbabwe May and Dec. Solitary, nesting exclusively in subterranean sites such as wells or pits, typically in *Brachystegia* woodland and usually 3-9 m below ground on slight overhang; new nest built every season. Nest U-shaped, of twigs 2-3 cm long with 1 or 2 feathers, measuring 60-80 mm wide × 25-65 mm deep, 3 eggs, though 2 recorded; parent incubates facing wall; estimated incubation 14 days; young fully feathered at 3 weeks, some leaving nest at 4 weeks and clinging to adjacent wall; fly at 5-5-6 weeks. Perhaps double-brooded; females probably not sexually mature until after 2 years old.

Movements. Resident throughout range, but apparently more abundant in Zambia in dry season, while numbers reduced in Zimbabwe in middle of wet season.

Status and Conservation. Not globally threatened. Only locally common even in areas of greatest abundance, and rare through much of range. Classified as Red Data species in South Africa where thought to number less than 50 pairs in 1984; in recent times, regularly recorded in N sector of Kruger National Park. Present, in small numbers, in Lengwe National Park, Malawi. Within Kenya commonest in coastal strip.

Bibliography. Ash & Miskell (1998), Aspinwall (1980a), Benson & Benson (1977), Benson *et al.* (1971), Borrett & Brooke (1967), Brooke (1966, 1968, 1969a, 1971c, 1971i, 1984), Donnelly (1974), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Fry *et al.* (1988), Garino (1996), Ginn *et al.* (1989), Harrison *et al.* (1997), Lewis & Pomeroy (1989), Lippens & Wille (1976), Mackworth-Præd & Grant (1957, 1962, 1970), Maclean (1993), Newman *et al.* (1992), Pinto (1983), Short & Horne (1985), Short *et al.* (1990), Snow (1978), Woods (1962), Zimmerman, D.A. *et al.* (1996).

Genus *HIRUNDAPUS* Hodgson, 1837

53. White-throated Needletail

Hirundapus caudacutus

French: Martinet épineux **German:** Stachelschwanzsegler **Spanish:** Vencejo Mongol
Other common names: White-throated Spinetail/Spinetailed Swift, (Northern) Spine-tailed Swift, Needle-tailed Swift, Northern Needletail

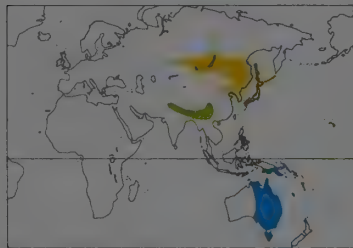
Taxonomy. *Hirundo caudacuta* Latham, 1801, New South Wales, Australia.

Genus formerly merged into *Chaetura*. Forms superspecies with *H. cochinchinensis*, with which in past sometimes considered conspecific. *H. cochinchinensis formosanus* formerly placed in present species, but has been shown to be virtually identical to nominate race of *H. cochinchinensis*, to which it clearly belongs. Two subspecies recognized.

Subspecies and Distribution.

H. c. caudacutus (Latham, 1801) - C Siberia E to Japan and Kuril Is; winters in S New Guinea and E Australia.

H. c. nudipes (Hodgson, 1837) - Himalayas, irregularly from N Pakistan E to Assam; Arunachal Pradesh through N Myanmar to SC China (Sichuan to Yunnan).



Descriptive notes. 19-20 cm; 101-140 g. Large swift with short square tail and weak, short rectrix spines protruding up to 6 mm beyond web; long full body and long broad wings; dark wings with blue gloss fading to green on remiges and coverts; off-white mantle, contrastingly white throat, white forehead, and white "horseshoe" mark on flanks and undertail-coverts on otherwise brown body. Rather variably plumaged juvenile less glossy with darker throat, less obvious mantle patch, black tips to undertail-coverts and usually dark forehead. Race *nudipes* has black forehead and lores, less distinct mantle patch and

generally darker plumage.

Habitat. In N parts of range, wooded lowlands and sparsely vegetated hills. In Himalayas at 1250-4000 m, feeding over river valleys and upland meadows and pastures, as well as subtropical, broadleaved and temperate forest between 1000-2800 m in C Bhutan. Winters in both coastal and mountainous areas. In Snowy Mts, Australia, abundant wintering over 1800 m, and common at 1530-1800 m. In Wallacea recorded from sea-level to 800 m on Sangihe, 500 m on Buru and 3000 m on Lombok, these mountains being free of snow. Recorded in low numbers over woodland in Brisbane Forest Park, Australia. In lowland rainforest zone of Papua New Guinea recorded over forest edge and non-forest.

Food and Feeding. Coleoptera, Hemiptera and Hymenoptera recorded for race *nudipes*. Wintering birds in New South Wales, Australia, recorded feeding on flying ants. Gregarious, but rarely associates with other species while foraging during breeding season.

Breeding. Gravid female *nudipes* collected in mid-Apr in N Cachar, N India; laying late May to early Jun in Siberia and Japan. Breeds Ussuriland late May to early Jun; eggs laid from mid-Jun and fledglings leave nest late Jul to early Aug. Nest consists of scrape in debris at bottom of tree hollow; 2 pairs apparently recorded prospecting old woodpecker hole in an *Acer* tree in Pakistan. Clutch 2-7; incubation begins with first egg, both sexes incubating, period 40 days, chicks blind and naked on hatching; fledging period 40-42 days.

Movements. Nominative race is a long-distance migrant. Himalayan race *nudipes* may be resident or perhaps just summer visitor; reported to appear and disappear at localities rather suddenly, making clear assessment of migratory status complicated. Nominative on Siberian breeding grounds mid-May to late Sept. L. Baikal from second half of May to late Aug; summer visitor, Japan, Apr-Sept; migrates through China, Indochina, and to lesser extent E Thailand, Wallacea and New Guinea; recorded on passage and possibly as winter visitor through Wallacea: mid-Oct, Sangihe; Oct to early Apr, Sulawesi; Oct, Taliabu (Sula Is); Nov and Feb, Buru; late Apr, Halmahera; Jan and early Apr, Lombok; late Sept, Oct and Jan, Flores; Oct, Timor; recorded from Aru in early Apr. Migrates through SE Asia Sept-Nov and winters in Australia Dec-Mar; many records of overshooting birds in New Zealand, Nov-Mar. Recorded from Cape York Peninsula, N Australia, with *Apus pacificus* in Jul, presumably non-breeding birds. In spring, recently recorded for first time on Hainan, Apr; migrates through Hong Kong mid-Mar to early May, SE Asia as late as May, and NE China in May.

Vagrant to Aleutian Is (4 records, May), Seychelles, and W & N Europe, with British and Irish records Apr-Jul and Nov; also one Nov record from Malta.

Status and Conservation. Not globally threatened. Race *nudipes* local and uncommon throughout most of range, though fairly common in C Bhutan. Nominative race becomes commoner farther E within Siberian range. Abundant in some areas of Australian winter quarters.

Bibliography. Ali & Ripley (1983), Ali *et al.* (1996), Ashburner (1985), Bailey & Sorensen (1962), Balsh (1980), Beehler, Pratt & Zimmerman (1986), Beehler, Sengo *et al.* (1995), Blackburn (1970), Blakers *et al.* (1984), Brazil (1991), Chantler (1993), Cheng Tsohsin (1987), Coates (1985), Coates & Bishop (1997), Collins & Brooke (1976), Corben *et al.* (1982), Coventry (1989), Cramp (1985), Day (1993), Dementiev & Gladkov (1951), Diamond & Bishop (1994), Driessens (1994), Dudley *et al.* (1996), Etchécopar & Hue (1978), Ferguson-Lees (1960), Flint *et al.* (1984), Gizenko (1955), Grimmett *et al.* (1998), Higgins (1999), Hudson (1968), Inskipp, C. & Inskipp (1991), Inskipp, T. *et al.* (1996), Knystautas (1993), Lekagul & Round (1991), Lepesch (1993), Lobko-Lobanovski (1956), Luleyeva (1993), MacKinnon & Philipps (1993), Medway & Wells (1976), Miller (1980), Neufeldt & Ivanov (1960), Osborne & Green (1992), Pettigrew & Wilson (1985), Quested (1980, 1982), Reilly (1991), Roberts (1991), Robson (1995b, 1997a), Robson *et al.* (1998), Rogacheva (1992), Rose (1997b), Slater (1995), Smith (1977), Smythies (1981), Snow & Perrins (1998), Stepanyan (1990), Strahan (1994), Tarburton (1993c), Tymstra *et al.* (1997), Wells (1999), White & Bruce (1986), Yamashina (1930, 1982), Zhao Zhengjie (1995).

54. Silver-backed Needletail

Hirundapus cochinchinensis

French: Martinet de Cochinchine **German:** Graukehlsegler **Spanish:** Vencejo de la Cochinchina
Other common names: White-vented/Silver-backed Spinetail/Spinetailed Swift, White-vented/Grey-throated Needletail; Rupchandi's Needletail (*rupchandi*)

Taxonomy. *Chaetura cochinchinensis* Oustalet, 1878, Saigon, Vietnam.

Genus formerly merged into *Chaetura*. Forms superspecies with *H. caudacutus*, with which in past sometimes considered conspecific. Race *rupchandi* has been listed as a megasubspecies. Race *formosanus* formerly placed in *H. caudacutus*, but has been shown to be virtually identical to nominate race of present species, to which it clearly belongs; indeed, may be better treated as synonymous with nominate, as grounds for racial split appear to be merely its isolated distribution. A single specimen from W Java, previously separated as form *ernsti* and variously treated as a distinct species or a race of *H. giganteus*, now synonymized with nominate race of present species. Three subspecies currently recognized.

Subspecies and Distribution.

H. c. rupchandi (Biswas, 1951) - C Nepal; winters W Java, Sumatra and peninsular Malaysia.

H. c. cochinchinensis (Oustalet, 1878) - NE India (Arunachal Pradesh, Assam, Meghalaya, Manipur and possibly Mizoram), N Myanmar and SC China (Hainan), and scattered localities (status unclear) in Thailand, Laos and Vietnam; winters in Thailand, Peninsular Malaysia, Sumatra and W Java.

H. c. formosanus (Yamashina, 1936) - Taiwan; wintering area unknown.



Descriptive notes. 20 cm; 76-86 g. Large swift with broad wings, short squarish tail with rectrix spines longest and strongest in centre and up to 6-5 mm beyond web, and long full body with head particularly prominent. Markings similar to *H. caudacutus*, differing in less contrasting throat-patch, usually slightly paler chest, less contrasting mantle-patch and grey-white tertial spots. Juvenile has less obvious pale saddle and some brown crescents on white areas of rear underbody. Race *rupchandi* has darker throat than nominate and slightly paler underparts, with less glossy upperparts; *formosanus* recognized

only by virtue of geographical isolation.

Habitat. To 600 m in C lowlands of Nepal, most frequently over primary forest. Winters over variety of habitats from lowlands to 3350 m, mainly in forest areas, especially close to water.

Food and Feeding. Often encountered feeding over water on newly hatched insects, frequently with *H. giganteus*. Highly mobile and often seen in small groups; up to 200 recorded together in Malaysia. Remains in an area for long only if feeding conditions very favourable.

Breeding. Nest unknown.

Movements. Poorly understood. Occurs in Malaysia late Sept to mid-Apr, with presumed migration through SE Asia Apr-May and Sept-Oct; collected at night from Fraser's Hill, W Malaysia, between late Oct and early Dec. Flocks of 20 on passage Bintan, Riau Archipelago, Strait of Malacca, late Nov, and 50-60 at lower Ketahun R, Sumatra, early Oct. Spring migration through Hong Kong late Mar to mid-May, with records from Vietnam in May.

Status and Conservation. Not globally threatened. Believed to be common in Assam Hills, otherwise status little known. Race *formosanus* said to be uncommon; nominate race rare on Hainan. Status uncertain in several areas, especially in Indochina, where many records may refer to passage birds; reported to be common in parts of SC & S Laos. Recorded in a number of protected areas, e.g. Chitwan National Park (Nepal), Khao Yai National Park (Thailand), Taman Negara National Park (Malaysia), Bukit Timah Nature Reserve (Singapore) and Nam Bai Cat Tien National Park (Vietnam).

Bibliography. Ali & Ripley (1983), Baker (1934a), Biswas (1951), Chantler (1993), Cheng Tsohsin (1987), Collins & Brooke (1976), Delacour (1947), Delacour & Jabouille (1951), Etchécopar & Hue (1978), Grimmett *et al.* (1998), Holmes (1996), Inskipp, C. & Inskipp (1991), Inskipp, T. *et al.* (1996), Lekagul & Round (1991), MacKinnon (1988), MacKinnon & Philipps (1993), van Marle & Voous (1988), Medway & Wells (1976), Mees (1971, 1973, 1985a), Parrott & Andrew (1996), Ripley (1982), Robson (1995d, 1997c), Robson *et al.* (1989), Smythies (1944), Thewlis *et al.* (1996), Vaurie (1965), Wells (1999), Zhao Zhengjie (1995).

55. Brown-backed Needletail

Hirundapus giganteus

French: Martinet géant **German:** Eilsegler **Spanish:** Vencejo Gigante
Other common names: Brown/Giant (Brown) Needletail, Brown/Brown-throated Spinetail/Spinetailed Swift

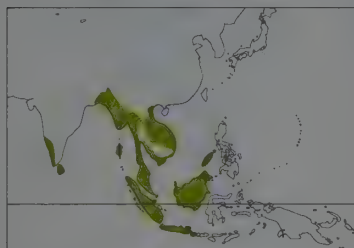
Taxonomy. *Cypselus giganteus* Temminck, 1825, Java.

Genus formerly merged into *Chaetura*. Forms superspecies with *H. celebensis*, with which in past sometimes considered conspecific. A single specimen from W Java, previously separated as form

ernsti and variously treated as a distinct species or a race of present species, now synonymized with *H. cochinchinensis cochinchinensis*. Two subspecies normally recognized.

Subspecies and Distribution.

H. g. indicus (Hume, 1873) - SW India and Sri Lanka, and Bangladesh E into SE Asia, and Andaman Is. *H. g. giganteus* (Temminck, 1825) - Malay Peninsula, Greater Sundas and Palawan (SW Philippines).



Descriptive notes. 25 cm; 123-167 g. Very large swift with broad wings, pinched in at body, broad protruding head and bulky hind-body, short tail with prominent rectrix spines protruding up to 11.5 mm beyond web in central tail; black-brown upperbody with pale brown saddle; indistinctly paler brown throat on dark brown underparts, which show distinct white horseshoe mark on undertail-coverts and rear flanks. Juvenile has narrow pale fringes to remiges and some brown crescents on horseshoe. Race *indicus* averages shorter-winged and has a whitish supraloral patch, which is somewhat reduced in juvenile.

Habitat. In Thailand over a wide range of habitats, mainly in lowlands, to 1800 m. Prefers primary forest but also seen over secondary forest, especially where lakes or rivers present. Recorded from moist deciduous forest at Mudumalai Wildlife Sanctuary, India.

Food and Feeding. Predominantly Coleoptera, Hemiptera, Orthoptera and Hymenoptera recorded for race *indicus*. Gregarious and often seen with other needletails. Forages over forest canopy and in particular takes advantage of insect hatchings over waterways and lakes.

Breeding. Season Feb-Apr, Kerala, S India. Solitary nester. No nest construction recorded, but a depression is used or made in debris at base of tree hollow and lined with dry leaves and straw, with access to hollow through natural hole or one made by woodpecker, positioned c. 15 m above ground. Clutch 3-4, occasionally 5.

Movements. Race *indicus* partial migrant, wintering in Malay Peninsula and probably Borneo; also possibly Sumatra, where present Sept-May. Nominate race resident.

Status and Conservation. Not globally threatened. Commonly encountered in suitable habitat. Deforestation with resultant loss of mature trees in which it nests indicates that populations may decline in parts of its range. Probably under-recorded in Indochina with first C Vietnamese records from N Annam in 1988 and from C Annam as recently as 1991; recently found to be common in C & S Laos, and apparently present all year round, though previously only listed for the NE of the country. Recorded in a number of protected areas, e.g. Indira Gandhi National Park (India), Khao Yai National Park (Thailand), Taman Negara National Park (Malaysia) and Cuc Phuong National Park (Vietnam).

Bibliography. Ali (1953), Ali & Ripley (1983), Baker (1934a), Bangs & Van Tyne (1931), Chakravarthy & Purna Chandra Tejasvi (1992), Chantler (1993), Collins & Brooke (1976), Daniels (1997), Davison (1992), Deignan (1945), Dickinson *et al.* (1991), Duckworth & Kelsh (1988), Grimmett *et al.* (1998), Henry (1998), Holmes (1996), Inskipp *et al.* (1996), Kannan (1998), Lekagul & Round (1991), MacKinnon & Phillips (1993), van Marle & Voous (1988), Medway & Wells (1976), Parrott & Andrew (1996), Phillips (1978), Primrose (1921), Riley (1938),

Robson, Eames, Nguyen Cu & Truong Van La (1993), Robson, Eames, Wolstencroft *et al.* (1989), Round (1988), Smith (1977), Smythies (1981, 1986), Stewart (1913), Thewlis *et al.* (1996), Tikader (1984), Wells (1999).

56. Purple Needletail

Hirundapus celebensis

French: Martinet des Célèbes

German: Purpursegler

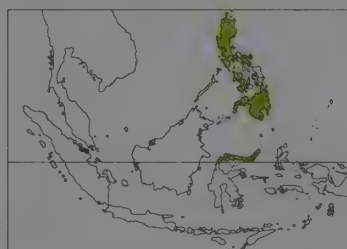
Spanish: Vencejo de Célebes

Other common names: Celebes Needletail, Sulawesi Spinetail/Spinetailed Swift

Taxonomy. *Chaetura gigantea* var. *celebensis* P. L. Sclater, 1865, Menado, Sulawesi.

Genus formerly merged into *Chaetura*. Forms superspecies with *H. giganteus*, with which in past sometimes considered conspecific. Some authors divide population into races *celebensis* (Sulawesi) and *dubius* (Philippines); a further body of opinion recognizes additional race *manobo* (Mindanao, Basilan, Negros). Monotypic.

Distribution. N Sulawesi and N & E Philippines (absent from Palawan).



Descriptive notes. 25 cm; 170-203 g. Very large swift with long, broad wings pinched in sharply at body, protruding head and bulky rear body; short tail with rectrix spines up to 4.5 mm beyond web in central tail; black plumage with purple gloss, uniform across body, except white supraloral patch and white horseshoe mark on rear flanks and undertail-coverts. Juvenile has dull brown supraloral patch and dull brown fringes to greater underwing-coverts.

Habitat. Occurs over open country and forests in hills and lowlands. In Sulawesi recorded at 150-2000 m.

Food and Feeding. Recorded taking large

numbers of bees from close to hives in Philippines.

Breeding. Not known.

Movements. Presumed resident. May be locally nomadic on Sulawesi.

Status and Conservation. Not globally threatened. Lack of museum specimens suggests scarcity. Large flocks of a species of *Hirundapus* recorded in C Sulawesi were presumably this species, which is generally uncommon but locally numerous in Sulawesi. In Philippines, observations from 1969 indicate heavy human persecution due to species' propensity for feeding on bees close to hives, though seen in good numbers on Negros in 1991. Occurs in Lore Lindu National Park (Sulawesi) and Mount Canlaon National Park (Philippines).

Bibliography. Andrew & Holmes (1990), Brooks & Dutson (1997), Brooks, Evans *et al.* (1992), Brooks, Magsalay *et al.* (1995), Coates & Bishop (1997), Collins & Brooke (1976), Danielsen *et al.* (1994), Delacour & Mayr (1946), Dickinson *et al.* (1991), Dutson *et al.* (1992), Evans, Dutson & Brooks (1993), Holmes & Philipps (1996), Inskipp *et al.* (1996), Mees (1985a), Morse & Laigo (1969), Rozendaal & Dekker (1989), Watling (1983), White & Bruce (1986).



PLATE 41

Family APODIDAE (SWIFTS) SPECIES ACCOUNTS

Genus *CHAETURA* Stephens, 1826

57. Band-rumped Swift

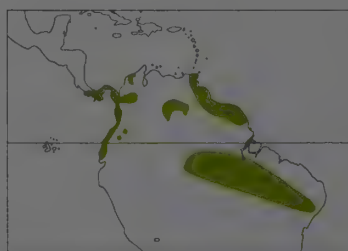
Chaetura spinicauda

French: Martinet spinicaude German: Dornensegler Spanish: Vencejo Lomiblanco
Other common names: Smoky Swift (*fumosa*)

Taxonomy. *Cypselus spinicaudus* Temminck, 1839, Cayenne. Formerly placed in genus *Acanthylis* with following three species. Race *fumosa* previously given species status. Five subspecies currently recognized.

Subspecies and Distribution.

- C. s. fumosa* Salvin, 1870 - Costa Rica, W Panama and N Colombia.
- C. s. aetherodroma* Wetmore, 1951 - E Panama to S Ecuador.
- C. s. spinicauda* (Temminck, 1839) - E Venezuela, the Guianas and N Brazil (N Amapá).
- C. s. latirostris* Zimmer & Phelps, 1952 - S Venezuela to Brazilian border and Delta Amacuro.
- C. s. aethalea* Todd, 1937 - C Brazil.



Descriptive notes. 10.5 cm; 16 g. Smallish swift with short square tail, rectrix spines up to 5 mm beyond web; protruding head; typical wing shape for genus with hooked wing-tips and broad midwing pinched in at body. Black-brown upperparts with contrastingly white rump band; uniformly dark underparts with throat slightly paler. Race *fumosa* darker with more distinct pale throat and larger, greyer rump patch; *aetherodroma* similar to latter but smaller; *latirostris* darker than nominate but paler below than last two races, with diagnostic large broad bill with more gently curved culmen; *aethalea* larger and darker with

broader, greyer rump and more pronounced throat patch.

Habitat. Main habitats defined as edge of lowland tropical evergreen forest and secondary forest. Occurs over a wide altitudinal range from sea-level to 1500 m, but in W Andes more restricted to montane sites at and above 300 m. In Amazonia over both lowland and highland forests and cleared areas, but N of Orinoco in Venezuela only over open habitats, down to sea-level.

Food and Feeding. Often feeds in crepuscular period over water. Single-species flocks most frequent at higher altitude. Forms feeding flocks with *C. cinereiventris*, *Cypseloides rutilus* and *Panyptila*

cayennensis, occurring primarily in lower strata of mixed flocks. Wet-season Panama study showed that Diptera, Hymenoptera and Coleoptera predominated with lesser numbers, less than 5% of total diet, of Hemiptera (Heteroptera and Homoptera) and a single spider. Sometimes takes insects and spiders from outer branches of trees by hovering briefly.

Breeding. Feb-Jun on Trinidad; in breeding condition on lower R Cauca, Colombia, in Mar; aerial copulation and birds in breeding condition in Panama Feb-Mar. On Trinidad nests in hollow trees.

Movements. Resident.

Status and Conservation. Not globally threatened. Often commonest *Chaetura* in areas of intrageneric sympatry. Considered most abundant swift in lowland Costa Rica and S Venezuela; recorded as common to uncommon in Ecuador. Present in many protected areas, e.g. Corcovado National Park and Carara Biological Reserve (Costa Rica), Río Nambí National Reserve (Colombia), Cueva del Guácharo National Park and Imataca Forest Reserve (Venezuela), Asa Wright Nature Centre (Trinidad).

Bibliography. Boesman (1998), de Carvalho (1961), Chantler (1995b), Chapman (1917), Dick *et al.* (1984), Friedmann (1948), Haverschmidt & Mees (1994), Herklots (1961), Hespénheide (1975), Hilty & Brown (1986), Marín (1993), Marín *et al.* (1992), Meyer de Schauensee & Phelps (1978), Peres & Whittaker (1991), Ridgely & Gwynne (1989), Ridgway (1911), Rogers (1939a), Salaman & Gandy (1994), Sick (1993, 1997), Slud (1964), Snow (1962a), Snyder (1966), Stiles & Skutch (1989), Stotz *et al.* (1996), Teixeira *et al.* (1986), Todd (1937b), Wetmore (1968a), Zimmer & Phelps (1952).

58. Lesser Antillean Swift

Chaetura martinica

French: Martinet chiquesol **German:** Antillensegler **Spanish:** Vencejo de Martinica

Taxonomy. *Hirundo martinica* Hermann, 1783, Martinique.

Forms superspecies with *C. cinereiventris* and *C. egregia*, and these three previously placed in genus *Acanthylis* along with *C. spinicauda*. Monotypic.

Distribution. Lesser Antilles, on Guadeloupe, Dominica, Martinique, St Lucia and St Vincent.



Descriptive notes. 10.5 cm. Smallish swift with short square tail, rectrix spines up to 5 mm beyond web, protruding head and distinctive wing shape, with hooked outer wing, bulging midwing and cutting in at body. Black-brown upperparts with narrow grey rump-band; brown underparts with indistinctly paler throat.

Habitat. Main habitats defined as tropical lowland evergreen forest and probably secondary forest. Seen over a variety of open and wooded habitats but mainly a forest species, in both lowland and hilly areas.

Food and Feeding. Gregarious forager, typically in flocks of 20-40, often with hirundines.

Breeding. Season believed to be late spring to early summer. Nest believed to be half-cupped; presumably nest-sites typical of genus, though 1 nest recorded in disused oven. 3 eggs.

Movements. Generally resident. Recorded as a vagrant to Nevis. Erroneous record from Trinidad.

Status and Conservation. Not globally threatened. Restricted-range species: present in Lesser Antilles EBA. Fairly common on Dominica, Martinique, St Lucia and St Vincent; uncommon on Guadeloupe.

Bibliography. Anon. (1998a), Bond (1956a, 1985), Chantler (1995b), Keith (1997), Raffaele *et al.* (1998), Ridgway (1911), Stattersfield *et al.* (1998), Stotz *et al.* (1996).

59. Grey-rumped Swift

Chaetura cinereiventris

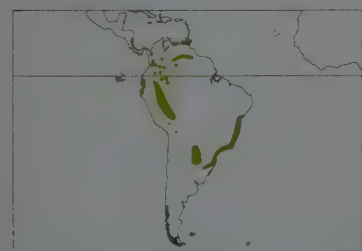
French: Martinet à croupion gris **German:** Graubürzelsegler **Spanish:** Vencejo Ceniciento
Other common names: Sclater's Swift; Ashy-rumped Swift (*sclateri*)

Taxonomy. *Chaetura cinereiventris* P. L. Sclater, 1862, Bahía.

Sometimes considered conspecific with *C. egregia*, and these two form superspecies with *C. martinica*; these three previously placed in genus *Acanthylis* along with *C. spinicauda*. All races but nominate have been grouped together in what might be incipient species, *C. sclateri*. Seven subspecies recognized.

Subspecies and Distribution.

C. c. phaeopygos Hellmayr, 1906 - E Nicaragua to Panama.
C. c. occidentalis Berlepsch & Taczanowski, 1884 - W Colombia, W Ecuador and extreme NW Peru.
C. c. schistacea Todd, 1937 - E Colombia to W Venezuela.
C. c. lawrencei Ridgway, 1893 - N Venezuela and S Caribbean Is.
C. c. guianensis Hartert, 1892 - E Venezuela and W Guyana.
C. c. sclateri Pelzeln, 1868 - S Venezuela through S Colombia, NW Brazil (upper Amazonia) and E Peru to NW Bolivia.
C. c. cinereiventris P. L. Sclater, 1862 - E Brazil, Paraguay and NE Argentina (Misiones).



Descriptive notes. 10.5 cm; 19 g. Smallish swift with short square tail, rectrix spines up to 7 mm beyond web, protruding head and distinctive wing shape, with hooked outer wing and bulging midwing cutting in at body. Glossy black upperparts including tail, with broad grey rump and proximal uppertail-coverts; underparts light grey, darker only on undertail-coverts. Races *guianensis* and *lawrencei* similar, latter slightly darker below and typically with strong contrast between black undertail-coverts and mid-grey belly; *schistacea* as latter but underparts deep grey and upperparts darker with steely-blue gloss; *occidentalis* and *sclateri* dark forms, latter with greyer belly, with darkest rumps and blackish-grey underparts beneath upper breast; *phaeopygos* a dark form but undertail-coverts paler than in other races.

Habitat. Main habitats defined as tropical lowland evergreen forest, montane evergreen forest, flooded tropical evergreen forest and secondary forest. Occurs from sea-level to 1800 m, in Ecuador 200-1800 m, typically over slopes with forest or second growth; on Grenada over young secondary forest.

Food and Feeding. Flying ants, bees, wasps, beetles and flies taken. Feeds in lower strata of mixed flocks of swifts, which are often composed of congeners, as well as *Aeronautes* and *Streptoprocne*. Also associates with hirundines. Gregarious, usually seen in flocks of 20-40. Recorded hovering to catch insects from canopy.

Breeding. Collected in breeding condition in N Antioquia, Colombia, in Mar-Apr; breeds in SE Brazil from Sept/Oct to Feb/Mar and in Costa Rica Mar-Jul; thought to breed in Trinidad in rainy season. Nests in chimneys or similar structures with secluded vertical surfaces; nest half-cup, re-used and rebuilt at same site; birds observed carrying nesting material in bill; both adults incubate at night. Clutch 2-4.

Movements. Resident throughout much of range, though incompletely known. In Paraguay possibly a breeding species only, though recent studies indicate resident there and also in Misiones.

Status and Conservation. Not globally threatened. One of commonest *Chaetura* swifts throughout range, indeed abundant in some areas such as Río Negro Preserve, Colonia Libertad, Costa Rica. Occurs in several protected areas, e.g. Braulio Carrillo National Park (Costa Rica), Cueva del Guácharo National Park (Venezuela) and Iguazú National Park (Brazil/Argentina).

Bibliography. Anon. (1993a), Beebe (1949), Becker & López (1997), Belton (1984), Benstead *et al.* (1993), Best & Clarke (1991), Best *et al.* (1993), Bloch *et al.* (1991), Brooks, Barnes *et al.* (1993), Brooks, Clay *et al.* (1995), Canevari *et al.* (1991), Chantler (1995b), Chapman (1917), Cooper (1997), Giraudo *et al.* (1993), Graves & Zusi (1990b), Hayes (1995), Herklots (1961), Hilty & Brown (1986), Howell (1957), Krabbe & Somoza (1994), Madroño & Esquivel (1997), Marcus (1983), Marín (1993), Marín *et al.* (1992), Meyer de Schauensee & Phelps (1978), Parker & Remsen (1987), Parker *et al.* (1991), de la Peña (1994), Peres & Whittaker (1991), Raffaele *et al.* (1998), Ridgely & Gwynne (1989), Rogers (1939a), do Rosário (1996), Saibene *et al.* (1996), Scott & Brooke (1985), Sick (1948c, 1959, 1993, 1997), Slud (1964), Snow (1962a), Snyder (1966), Stiles & Skutch (1989), Stotz *et al.* (1996), Thomas (1990), Todd (1937b), Wetmore (1968a), Wunderle (1985), Zimmer (1953b).

60. Pale-rumped Swift

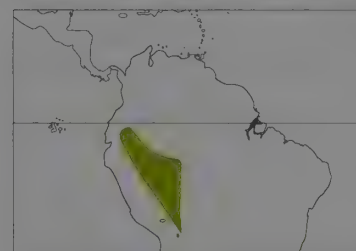
Chaetura egregia

French: Martinet de Bolivie **German:** Blaßbürtelsegler **Spanish:** Vencejo Egregio

Taxonomy. *Chaetura egregia* Todd, 1916, Río Surutú, Bolivia.

Sometimes considered conspecific with *C. cinereiventris*, and these two form superspecies with *C. martinica*; these three previously placed in genus *Acanthylis* along with *C. spinicauda*, and present species alternatively reported to be closely related to *C. spinicauda*. Monotypic.

Distribution. E Ecuador S through E Peru, W Brazil and NW Bolivia.



Descriptive notes. 10.5 cm; 23 g. Smallish swift with short square tail and rectrix spines extending beyond web, protruding head and distinctive wing shape, with hooked outer wing and bulging midwing, cutting in at body. Black upperparts with bronze gloss (blue in *C. cinereiventris*), whitish rump and proximal uppertail-coverts; pale throat on otherwise dark underparts; blackish undertail-coverts.

Habitat. Main habitat defined as tropical lowland evergreen forest. Occurs from lowlands to 1100 m. In Ecuador frequents lowlands and hills on E Andean slope, at altitude range of 200-1000 m; in N Peru recorded at 1050 m,

occurring over humid forest and more open landscapes.

Food and Feeding. Feeds mainly in lower strata of mixed flocks of swifts. Recorded with *C. cinereiventris*, *C. brachyura*, *Aeronautes montivagus*, *Cypseloides nylus* and *Panyptila cayennensis*.

Breeding. Not known. Three birds taken in Bolivia late Jun to early Jul were not in breeding condition.

Movements. Believed resident.

Status and Conservation. Not globally threatened. Presumed to be one of rarer *Chaetura* species and usually outnumbered by *C. cinereiventris* where they occur together. However, in San Martín and Amazonas, N Peru, commoner than *C. brachyura*, and considered to be abundant in upper elevations of Ecuadorian range. Present in Tambopata Reserve (Peru). Few museum specimens.

Bibliography. Brace *et al.* (1997), Chantler (1995b), Davis (1986), Marín (1993), Marín *et al.* (1992), Meyer de Schauensee (1982), O'Neill (1969), Parker & Remsen (1987), Remsen & Traylor (1989), Sick (1993, 1997), Stotz, Fitzpatrick *et al.* (1996), Stotz, Lanyon *et al.* (1997), Todd (1916).

61. Chimney Swift

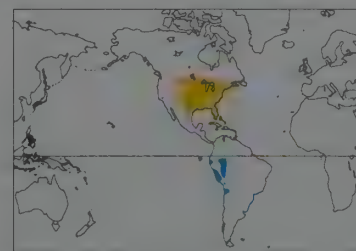
Chaetura pelagica

French: Martinet ramoneur **German:** Schornsteinsegler **Spanish:** Vencejo de Chimenea

Taxonomy. *Hirundo Pelagica* Linnaeus, 1758, South Carolina.

Previously considered conspecific with *C. vauxi* and *C. chapmani*. Recent study suggests that this species may be related to *C. andrei meridionalis*. Monotypic.

Distribution. E North America, and occasionally California and Arizona. Winters in E Ecuador, W & E Peru, NW Brazil and N Chile, though precise range unclear.



Descriptive notes. 12-14 cm; 21 g. Medium-sized swift with short square tail, rectrix spines up to 7.5 mm beyond web, protruding head and distinctive wing shape, with hooked outer wing and bulging midwing cutting in at body. Underparts dark grey-brown beneath pale to mid-grey throat, which can be white in some. Most uniform *Chaetura* with little contrast between rump/uppertail-coverts and rest of dark grey-brown upperparts.

Habitat. Though readily associated with urban settings, also forages and breeds over variety of natural habitats over wide range. Main habitats defined as river-edge forest, edge of tropical low-

land evergreen forest and second-growth scrub. In SW Peru mainly along coast and in W Andean valleys, where regular to 2500 m and sometimes to 3000 m over irrigated farmland and both suburban and even central city zones. In Ecuador recorded at 300-1000 m on E slope, 2500 m in Valle de Quito,

and 3200 m in S Ecuador. Migration in Mexico from sea-level to 1500 m. In California mainly in coastal lowlands, though in Owen's Valley a summering population occurs at 1200 m.

Food and Feeding. Hymenoptera and Diptera recorded, among other insects. Food pellet may contain over 200 insects. Recorded taking a weevil (Curculionidae) which may have been flightless, probably from foliage of sweetgum tree in grove where flock of 40-50 swifts were feeding by fluttering near outer branches or diving through open upper storey. Occupies lower strata in mixed swift foraging groups. Highly gregarious. Seen in association with *Aeronautes undecolus* in WC Peru. May forage by hovering briefly at branches to take insects and spiders. Observed apparently trying to steal dragonfly (Odonata) from Purple Martin (*Progne subis*).

Breeding. Eggs recorded Illinois mid-May to early Jul, New York late May to early Jul, Virginia late May to mid-Jul, and Quebec mid-Jun to early Jul. Typically nests in chimneys, though other structures used; recorded nesting in abandoned Pileated Woodpecker (*Dryocopus pileatus*) nesting hole, though tree nesting now very rare. Half-cup of twigs with semicircular saliva support, 75-113 mm wide, 25-31 mm deep and 50-75 mm front to back; nests in buildings typically placed high above floor in darkness. Copulation at nest-site; may also occur in flight. Clutch 2-7, average 4.0-5.3; incubation begins with laying of penultimate egg, period 19-21 days; females tend to cover eggs or young at night during first week; initially, several nestlings fed by regurgitation at each visit, later food pellet given to just 1 nestling; young fed on average every 30 minutes in first week, every 45 in second and then more erratically; feeding intervals as low as 14-5 minutes recorded; nest vacated between days 14 and 19, with first flight typically on day 30. Extra-parental co-operation well established, 1 colony recording this in 38% of breeding pairs: 22 threesomes and 6 foursomes. Hatching success 90-5%; overall breeding success 86% with 3-6 young fledging per breeding effort; 46-5% of adults in 1 study returned to study area, while only 11% of nestlings produced returned.

Movements. Present North America Apr-Sept. Migrates through West Indies late Aug to late Oct and mid-Apr to mid-May, through Panama Oct-Nov and in spring throughout Apr, and through Mexico mid-Mar to mid-May and late Aug to early Nov. Present SW Peru Nov-Apr. Recorded mid-Feb to early Mar in coastal cordillera of W Ecuador; may represent spring migratory stopover. Rarely recorded SE Farallon Is, 42 km W of San Francisco, late May to mid-Jun and mid-Sept to early Oct. Vagrant Bermuda, rare but regular, late Mar to late Apr and early Aug to late Dec; Bahamas, late Apr to early May and Oct; Galapagos Is and Greenland. Transatlantic vagrant to Britain, 4 records, late Oct to early Nov, and Tenerife (Canary Is). Probably under-recorded in N South America.

Status and Conservation. Not globally threatened. Common and widespread throughout most of range. Rare and occasional breeder in W North American range, where known to breed only since 1975 after first observation in 1930. Statistically significant downward trends in 12 US states, only Louisiana recording a small but significant increase during 1966-1995. Both Canadian and US populations showed statistically significant annual decreases of -0.9% and -5.8% respectively.

Bibliography. Amadon (1936), Amos (1991), Araya *et al.* (1973), Arvin (1993), Baicich & Harrison (1997), Bartlett (1952), Barton (1958), Beissinger & Osborne (1982), Bent (1940), Bloch *et al.* (1991), Blodgett & Zammuto (1979), Bowman (1952), Brown (1980), Buden (1987b, 1993), Byrne & Graves (1992), Cammace & Fischl (1985), Carter (1967), Chantler (1993), Coffey (1936, 1937, 1938, 1942, 1943, 1956, 1958), Collins & Bull (1996), Cyr (1995b), DeGraaf & Rappole (1995), Demetrio (1993), Devillers (1970), Dexter (1950, 1951a, 1951b, 1951c, 1952a, 1952b, 1952c, 1956b, 1961b, 1969, 1974, 1979, 1981, 1987, 1990, 1992), Driessens (1994), Duke (1977), Dunn (1979), Edwards *et al.* (1992), Evans & Drickamer (1994), Ferguson & Ferguson (1991), Fischer (1951, 1958), Fjeldså & Krabbe (1986, 1990), Ganier (1944), George (1971), Hilty & Brown (1986), Hofslund (1958), Howell & Webb (1995a), Huey (1960), Hughes (1988), Jackson (1997), James (1950), Johnsgard (1979), Johnson (1972), Johnston (1958), Kaufman (1996), Lincoln (1944), Lowery (1943), MacNamara (1918), Marín (1993, 1997a), Meyer de Schauensee & Phelps (1978), Meyers & Odum (1991), Michael & Chao Wansih (1973), Miller (1978), Monroe (1968), Moore (1946), Olson (1993), Parmalee & Klippel (1982), Pickens (1935a), Plenge (1974), Pyle & Henderson (1991), Raffaele *et al.* (1998), Ramsey (1970), Ridgely & Gwynne (1989), Ridgely (1991), Rogers (1939a), Shelly (1929), Sick (1993, 1997), Skutch (1935), Slud (1964), Small (1994), Snow & Perrins (1998), Spendlow (1985), Stewart & Kantrud (1972), Stiles & Skutch (1989), Stotz *et al.* (1996), Sutton (1927), Walcott (1974), Walker (1944), Weber & Theberge (1977), Wetherbee (1961), Wetmore (1957b, 1968a), Wetmore & Swales (1931), Williams (1986), Zammuto (1978), Zammuto & Franks (1978, 1979a, 1979b, 1981a, 1981b), Zammuto *et al.* (1981), Zimmer (1945a, 1953b).

62. Vaux's Swift

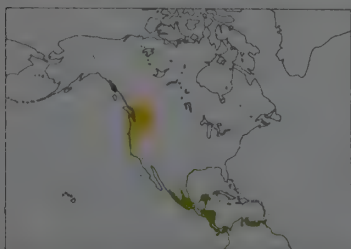
Chaetura vauxi

French: Martinet de Vaux **German:** Graubauchsegler **Spanish:** Vencejo de Vaux
Other common names: Dusky-backed Swift; Richmond's Swift (*richmondii*); Yucatán Swift (*gaumeri*)

Taxonomy. *Cypselus* [sic] *Vauxi* J. K. Townsend, 1839, Fort Vancouver, Washington. Previously considered conspecific with *C. pelagica* and *C. chapmani*. Races *richmondii* (including *ochropygia*) and *gaumeri* previously considered distinct species. A recent study considers that race *aphanes* is synonymous with *C. andrei andrei*, latter taking priority, i.e. as *C. vauxi andrei*, or that there may be two races of *C. vauxi* in N Venezuela, *aphanes* in W coastal range and *andrei* in E coastal range and S & E lowlands; same study also suggests that *aphanes* is identical to *richmondii*; however, these views not universally accepted. Six subspecies recognized.

Subspecies and Distribution.

- C. v. vauxi* (J. K. Townsend, 1839) - W North America from British Columbia to S California; winters in Mexico and Guatemala.
- C. v. tamaulipensis* Sutton, 1941 - E Mexico.
- C. v. gaumeri* Lawrence, 1882 - Yucatán Peninsula and Cozumel I.
- C. v. richmondii* Ridgway, 1910 - S Mexico to Costa Rica and W Panama (Chiriquí).
- C. v. ochropygia* Aldrich, 1937 - E Panama.
- C. v. aphanes* Wetmore & Phelps, Jr., 1956 - N Venezuela.



Descriptive notes. 12 cm; 18 g. Medium-sized swift with short square tail, rectrix spines up to 8 mm beyond web, protruding head and distinctive wing shape, with hooked outer wing and bulging midwing cutting in at body. Olive-brown upperparts, with rump and uppertail-coverts more distinctly paler than in *C. pelagica*; underparts extensively whitish on throat, becoming darker distally, being dark only on undertail-coverts. Race *tamaulipensis* generally darker with green-glossed blackish upperparts and darker underparts; *richmondii* has darker upperparts and underparts, more extensive black bristles in front of eye and

stronger rectrix spines; *ochropygia* has blacker upperparts, though rump shows greater contrast;

gaumeri smaller than nominate and *C. pelagica* and slightly paler than *richmondii* with weaker rectrix spines; *aphanes* a dark race similar to *richmondii*, though some *aphanes* from W Venezuelan coastal range have paler breast and belly than those from E coastal range.

Habitat. Found over wide range of habitats, including cloudforest at 1000 m in N Venezuela, arid areas of Central America, and both temperate and arid areas of Pacific coast in lowlands and mountains. Main Neotropical habitats defined as tropical lowland evergreen forest, montane evergreen forest, tropical deciduous forest, secondary forest and second-growth forest. In Costa Rica typically at 700-2000 m, recorded to 3000 m and also into lowlands on both slopes; in Panama specimens have been collected at 1280-2070 m and in Mexico from sea-level to 3000 m. In N Venezuela, population of *aphanes* in wet W coastal range may have different ecological requirements from that in deciduous seasonal forest in E coastal range (and *C. andrei andrei* in S & E lowlands). Recorded nesting at 1150 m in Montana. In Californian coastal lowlands breeds mainly below 300 m; in Yosemite National Park breeds 1200-2130 m and recorded foraging to 3650 m. In California mainly in redwood forests in narrow coastal zone, with infrequent records from Sierra Nevada. In NE Oregon 85% of nest-sites were in old growth, all in cavities used for roosting by Pileated Woodpeckers (*Dryocopus pileatus*), while Californian ranges of these 2 species appear correlated. A study of 160 forested stands in 1991 revealed that this swift was present in 41% of old-growth stands and only 8% of logged ones, reflecting increased availability of suitable nesting trees in old growth.

Food and Feeding. Often forages in large numbers, also with hirundines and other swifts. Frequently associates with *Streptoprocne zonaris* in Sierra de Tuxtla, Mexico, in flocks of 10-200. Often forages in evening, and feeds up to 5-5 km from nest. In natural forest habitat favours open airways such as rivers and roads. In breeding season various species of Homoptera, Diptera, Ephemeroptera and Hymenoptera recorded.

Breeding. Mating displays seen and enlarged gonads in specimens taken in Mar-Apr in Panama; breeds Mar-Apr-Jul in Costa Rica, and May-Jul in Venezuela; eggs early May to early Jul, most records mid-late Jun, in California; laying mid-Jun to early Jul, broods late Jun to early Aug, in British Columbia; chicks in nest in early Jul, C Honduras; tree-nesting pairs in NE Oregon built nests during Jun, eggs hatching from late Jun to early Jul and young leaving nest in early-late Aug, 28-30 days after hatching. Solitary or colonial. Disused chimneys preferred in British Columbia, though other sites include hollow maples (*Acer*); traditional sites often predominate; uses cavities made by Pileated Woodpeckers in many areas. Natural nests observed in Montana in old "topped" western hemlocks (*Tsuga heterophylla*) with central cavities, while old-growth stands of Douglas fir (*Pseudotsuga menziesii*) favoured in Cascade Range, Washington; in latter state old-growth grand firs (*Abies grandis*) also used, 8 nests being found in area of 2 ha. Access achieved by flying vertically down; one chamber was 7-3 m down with nest 1-5 m from bottom. Nest is half-cup bracket of grass and twigs agglutinated with saliva and stuck to vertical wall, 100 mm wide, 40 mm deep and 60 mm front to back. Clutch 1-7; chimney nest with 7 eggs in Montana was incubated continuously for 19 days, by both parents equally; brooding was continuous initially; nestlings fed every 10-35 minutes, compared with average of 12 minutes in NE Oregon study; weight of young rapidly increased until day 18, whence remained relatively stable until young left nest and declined until first flights undertaken; young left nest after 20-21 days, remaining in chimney for further 7 days before first flights; adults and young had completely vacated nest 3 days after initial flight, but roosting individuals, mainly young from nearby nests, were recorded at night after that day. Average breeding success 67%, with 4 young fledging per breeding effort.

Movements. Nominate race a migrant, present in far N of range May to mid-Sept, exceptionally late Mar on coast. Migrates through S California mid-Apr to early May, with weaker autumn passage peaking early Sept, though continuing to early Oct, migrants leaving the state by mid-Oct. Recorded SE Farallon Is, 42 km W of San Francisco, in similar numbers over 22 years, in spring 813 in early-late May, and in autumn 803 early Sept to late Oct. Recorded E to Louisiana and Florida. Passage through NW Mexico Apr-May and mid-Sept to Oct; nominate race present C Mexico to W Honduras, mid-Sept to May. Incidence of wintering in California increasing, small flocks occurring mainly in S, though wintering as far as NW California not unknown.

Status and Conservation. Not globally threatened. Common throughout most of range, though often locally, e.g. in Montana during 1970's considered common in Idaho county while rare in adjacent Fortine. Survey work during 1966-1995 in North America indicates significant decrease in Californian population (-4.9% p.a.) but no statistically significant overall decline in either Canadian or US population. It has been suggested that lack of suitable nest-sites, primarily hollow snags in many areas, limits range expansion. Indeed, fate of many North American populations may depend on sensitive forestry policy, as it has been suggested that elimination of old growth from managed forests could lead to regional extinction. Neotropical abundance varies, e.g. common in parts of Costa Rica but uncommon in parts of N Belize.

Bibliography. Alcorn (1988), Baicich & Harrison (1997), Baldwin & Hunter (1963), Baldwin & Zackowski (1963), Bent (1940), Binford (1989), Bull (1991), Bull & Beckwith (1993), Bull & Blumton (1997), Bull & Collins (1993a, 1993b, 1993c, 1996), Bull & Cooper (1991), Bull & Hohmann (1993), Bull & Torgensen (1993), Campbell *et al.* (1990), Chantler (1993), Collins (1967c, 1971), Collins & Bull (1996), Cooper (1997), Davis (1937), DeGraaf & Rappole (1995), Dickinson (1951), Dunn (1979), Edson (1931), Finley & Finley (1924), Fischer (1958), Fix (1988), Gaffney (1986), Gómez de Silva (1998), Griffie (1961), Griscom (1932a), Howell, S.N.G. & Pyle (1993), Howell, S.N.G. & Webb (1995a), Howell, T.R. (1957), Huey (1960), Jobin (1952), Kaufman (1996), Lee *et al.* (1996), Lowery (1939), Manna & Meslow (1984), Marín (1997a), McCrary *et al.* (1986), McNair & Lewis (1997), Meyer de Schauensee & Phelps (1978), Monroe (1968), Phillips & Webster (1957), Pyle & Henderson (1991), Ridgely & Gwynne (1989), Ridgway (1910, 1911), Rogers (1939a), Rosenberg & Terrill (1986), Rowley (1966), Schaldach (1963), Slud (1964), Small (1994), Stager (1965), Sterling & Paton (1996), Stiles & Skutch (1989), Stotz *et al.* (1996), Summers (1995b), Sutton (1941a, 1948), Sutton & Phelps (1948), Taylor (1905), Thompson (1977), Valley & Whitman (1997), Watson (1933), Wetmore (1957a, 1957b, 1968a), Weydemeyer (1975).

63. Chapman's Swift

Chaetura chapmani

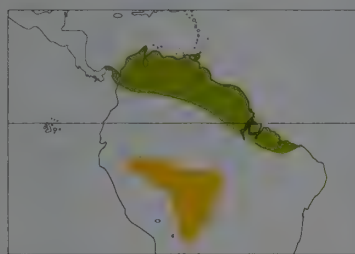
French: Martinet de Chapman **German:** Chapmansegler **Spanish:** Vencejo de Chapman
Other common names: Dark-breasted Swift

Taxonomy. *Chaetura chapmani* Hellmayr, 1907, Caparo, Trinidad.

Previously considered conspecific with *C. pelagica* and *C. vauxi*. Recent proposal to raise *viridipennis* to full species, but this is not universally accepted. Nominate race may consist of two disjunct populations, representing different races, one in lowlands from C Panama to N Colombia, the other from E Venezuela to NE Brazil, with intervening gap (W & N Venezuela) occupied by *C. vauxi*. Two subspecies recognized.

Subspecies and Distribution.

- C. c. chapmani* Hellmayr, 1907 - C Panama through Colombia, Venezuela and the Guianas to NE Brazil.
 - C. c. viridipennis* Cherrie, 1916 - E Peru, C & E Bolivia and W Brazil; winters to N Colombia.
- Descriptive notes.** 13-14 cm; 21.5-28 g. Medium-sized swift with short square tail, rectrix spines 6 mm beyond web, protruding head and distinctive wing shape, with hooked outer wing and bulg-



ing midwing cutting in at body. Glossy black upperparts with distinctly paler grey rump and uppertail-coverts; very uniform dark brown underparts. Race *viridipennis* larger. A recent study suggests that differences in gloss between subspecies result from age differences in specimens, and states that *viridipennis* differs from *C. andrei meridionalis* in culmen length and less contrasting and more uniform throat and rump coloration, and in having primaries P9 and P10 equal in length.

Habitat. Main habitats defined as tropical lowland evergreen forest, secondary forest and second-growth scrub. In Colombia occurs from

sea-level to 1600 m, in N Venezuela to 600 m and in S Venezuela to 200 m. Recorded throughout Trinidad, but prefers wooded terrain with hills and especially forested uplands. Also seen feeding close to sea-level over swamp and mangrove areas.

Food and Feeding. Forages in mixed flocks with *C. cinereiventris*, *C. spinicauda* and *C. brachyura*. Occurs in monospecific flocks in upper Rio Urucu, Amazonas, Brazil. Feeds close to ground in dense low cloud conditions.

Breeding. N nominate race breeds in wet season, late spring to early autumn; in Trinidad, nest in use early May to early Jun; *viridipennis* apparently breeds in austral summer. Known from 1 nest in Trinidad, 20 cm below top of cement manhole, in brushy savanna; half-cup nest 69 mm wide, 24 mm deep and 59 mm front to back. 2, possibly 3, eggs; incubation 17-18 days; young when less than 48 hours old flesh-pink, with traces of grey on bill and claws, lacking natal down, with whitish egg-tooth on tip of upper mandible, weight 1.5 g.

Movements. N nominate race resident within its range; *viridipennis* a transequatorial migrant, with Mar-Apr records from Antioquia, Colombia. Recorded late Aug. Los Fierros, Santa Cruz, E Bolivia.

Status and Conservation. Not globally threatened. One of rarer South American swifts with few specimens or observations over an apparently wide distribution; precise limits of breeding range not well known. However, recorded in 1960's with relative frequency in Val and Arima Valley, Trinidad. Commonly recorded in upper Rio Urucu, Amazonas, Brazil.

Bibliography. Bates *et al.* (1992), Cohn-Haft *et al.* (1997), Collins (1968a, 1968b), ffrrench & ffrrench (1966), Haverschmidt & Mees (1994), Herklots (1961), Hilty & Brown (1986), Kirwan & Sharpe (1999), Marin (1997a), Meyer de Schauensee & Phelps (1978), Peres & Whittaker (1991), Ridgely & Gwynne (1989), Rogers (1939a), Sick (1993, 1997), Snyder (1966), Stotz *et al.* (1996), Wetmore (1957b, 1968a).

64. Short-tailed Swift

Chaetura brachyura

French: Martinet polioüre **German:** Stutzschwanzsegler **Spanish:** Vencejo Rabón

Taxonomy. *Acanthylis brachyura* Jardine, 1846, Tobago.

Four subspecies recognized.

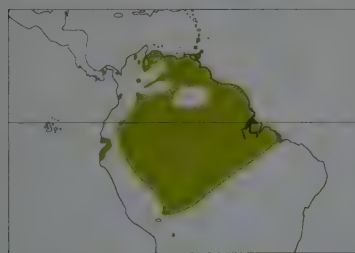
Subspecies and Distribution.

C. b. brachyura (Jardine, 1846) - Panama E to the Guianas and Trinidad, S to WC Brazil and N Bolivia.

C. b. praevelox Bangs & Penard, 1918 - Grenada, St Vincent and Tobago.

C. b. ocyptes Zimmer, 1953 - SW Ecuador and extreme NW Peru.

C. b. cinereocauda (Cassin, 1850) - NC Brazil.



Descriptive notes. 10 cm; 18 g. Smallish to medium-sized swift with protruding head, remarkably short square tail (wings appearing disproportionately long as a result), rectrix spines up to 5 mm beyond web, and distinctive wing shape, with hooked outer wing and deeply bulging midwing cutting in at body. Glossy purplish-black plumage, pale grey-brown distally from rump and vent. Race *praevelox* generally browner with slightly paler throat; *ocyptes* has longer tail and wings than other races and paler grey chin and throat, brown forehead and pale-fringed supercilary line; *cinereocauda* has even blacker throat than

nominate and generally green gloss.

Habitat. Main habitats defined as secondary forest, edge of tropical lowland evergreen forest, tropical deciduous forest and second-growth scrub. A lowland species recorded to 1900 m in Ecuador; recent studies showed presence at 200-1100 m on E Andean slope, though not usually seen above 800-900 m. Often seen on coast, especially over mangroves where it roosts, at least in Surinam; also over open areas, often arid but also llanos, and over primary or second-growth forest. In Villavicencio area of Colombia, restricted to remnant forest, morichales and second-growth where common. On Tobago over young secondary forest and scrub. Occasionally over human settlements.

Food and Feeding. Panamanian study showed that Diptera, Hymenoptera and Coleoptera predominated with lesser numbers (less than 5% of total diet) of Hemiptera (Heteroptera and Homoptera). Four specimens collected in Panama, during wet season, had been feeding on swarms of Hymenoptera. One stomach contained 384 fig wasps (Agaonidae) of 2 species and 160 ants of 3 species, among total catch of 702 prey items. Four spiders also recorded in 2 specimens from Panama. Food ball from Trinidad contained large number of spiders. Forages in lower strata of mixed swift flocks. Usually seen in small flocks, often with other *Chaetura* swifts. Pair studied in Trinidad believed to feed regularly 5 km from nest-site where feeding young. Takes insects and spiders from outer branches of trees by hovering briefly.

Breeding. In Trinidad breeds in summer rainy season, nesting rapidly after first rains early Apr to early Sept. Breeding initiated by May rains in Panama; male in breeding condition collected early Jun from Ayacucho, S Cesar, Colombia; colony of 8 pairs breeding in Bolivian chimney Sept-Nov. Started nesting in chimneys in 1930's. In main Trinidad study, 21 nest-sites were manholes and 1 a subterranean concrete walled room; in 4-month season made 1-3 breeding attempts, rarely 4, with interval of c. 4-74 days between ending previous attempt and starting new clutch. 2-7 eggs (average 3.8); incubation 17-18 days; hatching rates 51-5% of all eggs, 95% of those reaching expected hatching date; entire clutch hatched in 48-72 hours; initially long periods of brooding by day, becoming shorter but still 20-minute periods by day 8; nocturnal brooding, by 1 or both parents, until young too large to cover effectively, at c. 2 weeks; by day 2 both adults may be absent, probably foraging for young; most nestlings stayed in nest until 22-23 days after hatching and then clung to nest-cavity walls, where majority stayed until 30-36 days old; 53-5% of hatched young

successfully fledged. Average overall breeding success 27%, with 1-1 young fledging per breeding effort; predation by bats suspected.

Movements. Resident. Vagrant to St Croix, Puerto Rico.

Status and Conservation. Not globally threatened. Locally common throughout range, for example noted commonly over suitable habitat in Villavicencio area, Colombia, and in uplands of Reserva Ecológica de Loma Alta, Ecuador. Possible increase in some areas. Discovered in Panama as recently as 1960, where now known to be common in suitable habitat. Flock of c. 300 birds recently recorded in Choetó, NW Colombia, where species previously unknown.

Bibliography. Becker & López (1997), Beebe (1947, 1949), Best *et al.* (1993), Bloch *et al.* (1991), Bond (1956a), de Carvalho (1961), Collins (1967a), Davis (1986), ffrrench (1991), ffrrench & ffrrench (1966), Friedmann & Smith (1950), Haverschmidt (1958b), Haverschmidt & Mees (1994), Herklots (1961), Hilty & Brown (1986), Krabbe & Sornoza (1994), Marin (1993), McKay (1980), Meyer de Schauensee & Phelps (1978), Parker & Remsen (1987), Pearson (1975), Raffaele (1989), Raffaele *et al.* (1998), Ridgely & Gwynne (1989), Salaman & Gandy (1994), Sick (1993, 1997), Snow (1962a), Snow & Snow (1964), Snyder (1966), Stotz *et al.* (1996), Wetmore (1939, 1968a), Wunderle (1985), Zimmer (1953b).

65. Ashy-tailed Swift

Chaetura andrei

French: Martinet d'André **German:** Grauschwanzsegler **Spanish:** Vencejo de Tormenta
Other common names: André's/Southern Swift; Sick's Swift (*meridionalis*)

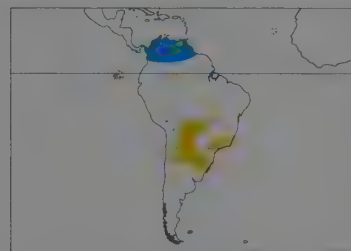
Taxonomy. *Chaetura andrei* Berlepsch and Hartert, 1902, Caicara, River Orinoco, Venezuela.

Recently suggested that nominate race be merged with *C. vauxi aphanes* (as *C. v. andrei*) and that *meridionalis* thus be given separate specific status. Several specimens formerly identified as *andrei* (e.g. from Carabobo, Falcón, Lara, Distrito Federal) are clearly *C. vauxi aphanes*, and of the 5 valid specimens of *andrei* 4 are from Bolívar (2 each from Caicara and Altigracia) and 1 from Sucre (San Félix); those birds mislabelled as *andrei* may either be post-breeding migrants of a *C. vauxi* population, perhaps from E part of Coastal Range, or may represent a resident form from hilly lowlands of S Venezuela; identification of 2 other specimens taken from near the Serranía de Imataca, S of Orinoco Delta, needs to be confirmed. Race *meridionalis* almost identical in plumage to *C. pelagica*, to which it may be closely related; best separated by differences in wing-formula, as P9 is 3-8 mm longer than P10 whereas in *C. pelagica* both are equal. Two subspecies recognized.

Subspecies and Distribution.

C. a. andrei Berlepsch & Hartert, 1902 - E Venezuela.

C. a. meridionalis Hellmayr, 1907 - E & SE Bolivia, SE & S Brazil, Paraguay and N Argentina; winters N to Panama, Colombia and French Guiana.



Descriptive notes. 13.5 cm; 21.5 g. Medium-sized swift with short square tail between *C. brachyura* and other *Chaetura* in length, and rectrix spines 2 mm beyond web; protruding head and distinctive wing shape, hooked in outer wing and with bulging midwing cutting in at body. Olive-brown upperparts with moderately contrasting paler grey rump/uppertail-coverts; diagnostic underpart markings, pale throat and relatively pale uppertail-coverts on otherwise dark brown underparts. Race *meridionalis* can have white throat; that race also much longer-winged and longer-tailed than nominate, wing mean 131.5 mm against

114.5 mm, tail mean 37 mm against 30-25 mm.

Habitat. Main habitats defined as edge of tropical lowland evergreen forest, secondary forest and second-growth scrub. Found from lowlands to 1600 m over wide range of habitats. Wintering *meridionalis* recorded over primary cloudforest from cordilleras of N Venezuela.

Food and Feeding. Typically in small foraging groups.

Breeding. Season end Aug-Jan S Brazil, Sept-Mar SE Brazil; nests Oct-Nov. Mato Grosso: lays late Nov, São Paulo state. Breeds commonly in chimneys and under eaves in urban areas and more naturally in hollow trees and buriti palms (*Mauritia*); site loyalty exhibited. Half-cup nest in buriti palm, of leaf stalks and often palm leaf fibres stuck with saliva to vertical wall; material may be collected from trees in flight, using feet; nest 85 mm wide, 37 mm deep and 43 mm front to back; re-used until it falls down, whereupon rebuilt on same spot. Clutch 3-4, less often 5; assumed that more than 1 female contributed to brood of 9 young in an attic nest, since other adults present at nest-site; both sexes undertake nesting duties; initially young fed intensely, with up to 61 feeds daily, declining as they mature. In São Paulo state, at least, timing of hatching seems to preclude possibility of second brood.

Movements. Race *meridionalis* at least partly migratory, crossing equator to reach Roraima from May; recorded in austral winter from Panama, N Colombia, Venezuela and Surinam, though scarcity there suggests some wintering occurs farther S, possibly among N breeding populations of this form. Arrives in breeding range early-mid Sept, earliest SE Brazil in late Aug. Irregular extended movements from breeding range up to mid-Apr. Non-breeding roost in Minas Gerais declines from Feb and species absent by mid-Apr. Difficult to ascertain post-breeding range, since at least part of breeding population in coastal Brazil may winter in that area or leave only briefly; few reliable winter records, with overlap of similar species. Breeding status in NE Brazil uncertain as birds may be at S limit of wintering range, N edge of breeding range, or just passing through. May overlap with *C. pelagica* in Bolivia and Argentina. Absent from Serra dos Orgãos (N of Rio) May to mid-Aug, from SE Brazil during coolest months, from Pocone (SW Mato Grosso) May-Nov, and largely from Paraguay during this season. Rarely recorded Bolivia, Feb and late Sept to early Oct. Colombian/Venezuelan llanos and Orinoco basin should be investigated as potential wintering grounds. Vagrant to S Rio Grande do Sul (Brazil) and Falkland Is.

Status and Conservation. Not globally threatened. Race *meridionalis* common within breeding range, though less often found within wintering range, and is most abundant Brazilian swift away from Amazon, though rare in Pocone; common in Paraguay. Occurs in Calilegua and El Rey National Parks (Argentina) and Itatiaia National Park and Nova Lombardia Biological Reserve (Brazil). Status of nominate race uncertain.

Bibliography. Abendroth (1953), de Andrade & de Freitas (1987), Belton (1984), Brooks *et al.* (1993), Canevari *et al.* (1991), Collins (1967c, 1968b), Contreras *et al.* (1990), Darlington (1931), Fjeldså & Mayer (1996), Haverschmidt & Mees (1994), Hayes (1995), Hilty & Brown (1986), Lowen, Barrina, Aiz & Tobias (1996), Marin (1997a), Maurício & Dias (1998), Meyer de Schauensee & Phelps (1978), Mitchell (1957), Norez *et al.* (1983), Oniki *et al.* (1992), de la Peña (1994), Phelps & Phelps (1958), Remsen & Traylor (1983), Remsen, Traylor & Parkes (1986), Ridgely & Gwynne (1989), Rogers (1939a), de Rosário (1996), Saibene *et al.* (1996), Short (1975), Sick (1948b, 1950b, 1959, 1993, 1997), Stotz *et al.* (1996), Wetmore (1926, 1968a).



PLATE 42

inches 5
cm 13

PLATE 42

Family APODIDAE (SWIFTS) SPECIES ACCOUNTS

Tribe APODINI

Genus *AERONAUTES* Hartert, 1892

66. White-throated Swift

Aeronautes saxatalis

French: Martinet à gorge blanche German: Weißbrustsegler Spanish: Vencejo Gorgiblanco

Taxonomy. *Acanthylis saxatalis* Woodhouse, 1853, Inscription Rock, New Mexico. Previously placed in *Apus*. Present species and *A. montivagus* apparently more closely related to each other than either is to *A. andecolus*. Two subspecies recognized.

Subspecies and Distribution.

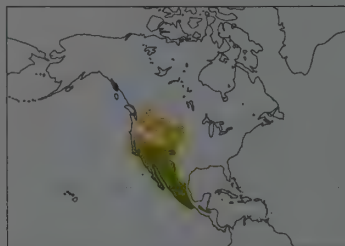
A. s. saxatalis (Woodhouse, 1853) - SW Canada S through W USA to S Mexico (Oaxaca) W of Caribbean lowlands.

A. s. nigrior Dickey & van Rossem, 1928 - S Mexico (Chiapas) to C Honduras.

Descriptive notes. 15-18 cm; male mean 34 g, female mean 32 g. Medium-sized swift with sharply pointed outer wing, broad inner wing and large, shallowly forked tail. Black upperparts with distinctive white trailing edge to secondaries, white forehead and supercilium; broad white throat, extending in strip to central vent area; isolated white patches on rear flanks; underparts

otherwise black. Female averages narrower white trailing edge. Race *nigrior* has wholly darker head.

Habitat. A montane species found to 3000 m in Mexico and 2450 m in Guatemala, but sometimes descending to 600 m in Honduras. In California breeds from lowlands to 2130 m in Yosemite National Park, with foraging recorded to 4270 m. Occurs around canyons and cliff-faces, both coastal and interior, and arid areas, though meadows important for foraging and species never breeds far from these. Importance of water indicated by 8-year study in Anza-Borrego Desert, California, where



despite mainly drought conditions creeks continued to flow and this species occurred in suitable canyons. Seen foraging over pinyon, yucca and creosote plant zones in Joshua Tree National Monument, California. Summer resident in Apache County, Arizona, occurring over grassland and around rocky cliffs; over a range of habitats on migration. Occurs as non-breeding insectivore in Chihuahuan desert, Mexico. Main Neotropical habitats defined as arid montane scrub, pine-oak forest and second-growth forest.

Food and Feeding. 21 stomachs contained Diptera, mainly Anthomyiidae, with fewer Dolichopodidae, Sarcophagidae and Bibionidae, Coleoptera, especially Aphodidae, Hymenoptera, and true bugs, mainly Pentatomidae, Membracidae, Cicadellidae and Coreidae. In 2 stomachs over 90% of prey insects were ants, and another stomach contained entirely march flies (Bibionidae). Recorded feeding on insects disturbed by combine harvester. Often highly gregarious.

Breeding. Laying early May to late Jun, peaking late May to early Jun, California; clutches recorded mid-May to early Jul and broods early Jun to mid-Aug, British Columbia. Colonial. May copulate in flight. Nests in suitable rock niches, on cliffs, including sea cliffs, beneath overhangs, and also in buildings where suitable holes present; will breed in disused hirundine nests; great site loyalty with continuous use over many decades. Cupped nest of grasses, moss and with some feathers, either self-supporting on vertical wall or placed on ledge; nest agglutinated with saliva which also secures it in place. Clutch 3-6 eggs.

Movements. Nominate race partial migrant. Present British Columbia in far N of range, early Apr to late Sept, most departing from late Aug. Migrant Californian population present mid-Mar to mid-Oct. Winters S California and Nevada where absent from coldest areas; it has been suggested that predominance of coastal winter records in Baja California suggests at least limited seasonal altitudinal movements. Most winter farther S, some as far as Honduras. Migrates in flocks, up to 50. Rarely recorded SE Farallon Is, 42 km W of San Francisco, during Apr and mid-late Oct. Race *nigrior* resident. Data from Belize unconfirmed.

Status and Conservation. Not globally threatened. Common throughout much of North American range, but rare in Mexico and uncommon in Honduras. Considered uncommon to fairly common in recent census of mountainous areas of S California and common in parts of Arizona. Recent survey work revealed slight yet significant decline (by 2.0% per annum) in USA during 1966-1995.

Bibliography. Alcorn (1988), Alden & Mills (1976), Austin & Rea (1976), Baieich & Harrison (1997), Baltosser (1986b), Bartholomew *et al.* (1957), Behle (1973, 1976), Bent (1940), Binford (1989), Campbell *et al.* (1990), Cardiff & Remsen (1981b), Collins (1973), Collins & Johnson (1982), Dawson (1923), DeGraaf & Rappole (1995), Dickey & van Rossem (1928), Dobkin *et al.* (1986), Enderson & Craig (1974), Fretwell (1978), Howell & Webb (1995a), Johansson & White (1995), Johnsgard (1979), Kaufman (1996), Lentz (1993), Lima (1993), Linsdale (1938), Massey (1994), McCrary *et al.* (1986), McNicholl (1975), Michael (1926), Monroe (1968), Oberholser (1920), Peterson (1990), Pickwell (1937), Preston (1986), Pyle & Henderson (1991), Raitt & Pimm (1976), Ridgway (1911), Rogers (1939b), Rohwer (1971), Root (1988), Rosenberg & Terrill (1986), Seyfert (1984), Small (1994), Stotz *et al.* (1996), Summers (1995a), Unitt *et al.* (1995), Weber (1975), Weydemeyer (1975).

67. White-tipped Swift

Aeronautes montivagus

French: Martinet montagnard **German:** Bergsegler **Spanish:** Vencejo Montañés
Other common names: Mountain Swift

Taxonomy. *Cypselus montivagus* d'Orbigny and Lafresnaye, 1837, Santa Cruz de la Sierra, Bolivia. Previously placed in *Apus*. Present species and *A. saxatilis* apparently more closely related to each other than either is to *A. andecolus*. Race *tatei* originally placed in monotypic genus *Duidia*. Two subspecies recognized.

Subspecies and Distribution.

A. m. montivagus (d'Orbigny & Lafresnaye, 1837) - Scattered range from N Venezuelan cordilleras S through Andes to NC Bolivia and NW Argentina.

A. m. tatei (Chapman, 1929) - *tepulis* of S Venezuela and extreme N Brazil.



Descriptive notes. 13 cm; 20 g. Smallish swift with broad inner wing, sharply pointed outer wing and large, shallowly forked tail; black-brown upperparts with narrow white trailing edge to secondaries and white tips to tail; underparts and much of face black with broad white throat-patch and white patches on vent and rear flank. Female lacks white tail-tips. Race *tatei* has glossed blue-black upperparts.

Habitat. Main habitats defined as montane evergreen forest, secondary forest and tropical lowland evergreen forest. A montane species of subtropical zones occurring over forest, both primary and second growth, and open slopes

at 500-2700 m in Andes, 1500-2700 m on W slopes of inter-Andean Zone, Ecuador, and 700-1900 m in *tepulis*; recorded to 3200 m in WC Andes. Not infrequently over human settlements, especially derelict buildings such as at Rancho Grande, N Venezuela, where large breeding colony; also, especially in poor weather, in valley bottoms including arid ones. In NW Argentina occurs over deep canyons, maintaining altitude in erratic wide circles before moving to another area to repeat operation; also noted with *Chaetura andrei* at 1700 m, Abra de Cañas.

Food and Feeding. Forages in lower strata in single-species or mixed swift flocks. Typically in flocks of up to 20.

Breeding. Breeds Apr-Jul, N Venezuela; seen entering possible nest-sites early Apr. Colombia; breeding in Valle de Guayllabamba, Ecuador, apparently not synchronized, evidence from collected birds suggesting some start breeding in Nov-Dec. Colonial. Nests in rock fissures in ravines and in holes in buildings, but no information on nest morphology, eggs or young.

Movements. Resident.

Status and Conservation. Not globally threatened. Locally common, indeed locally abundant, at least in Ecuador. Perhaps more widespread than hitherto believed, since recently recorded from new sites in Venezuela, and noted on several occasions since 1993 fin Calilegua National Park, NW Argentina.

Bibliography. Beebe (1949), Best *et al.* (1993), Boesman (1998), Chapman (1929, 1931), Davis (1986), Dickerman & Phelps (1982), Fjeldsá & Krabbe (1990), Fjeldsá & Mayer (1996), Friedmann (1948), Gilliard (1941), Hilty & Brown (1986), Kirwan (1996c), Marín (1993), Marín *et al.* (1992), Mazar, Clark *et al.* (1998), Meyer de Schauensee & Phelps (1978), Moschione (1993), Remsen & Traylor (1989), Salaman & Gandy (1994), Sick (1993, 1997), Stotz *et al.* (1996), Willard *et al.* (1991), Zimmer (1953b).

68. Andean Swift

Aeronautes andecolus

French: Martinet des Andes **German:** Andensegler **Spanish:** Vencejo Andino

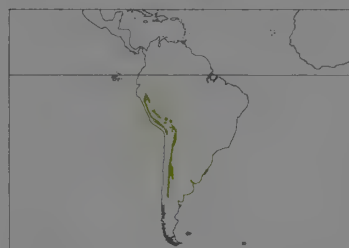
Taxonomy. *Cypselus andecolus* d'Orbigny and Lafresnaye, 1837, La Paz, Bolivia. Previously placed in *Apus*, even when *A. saxatilis* and *A. montivagus* were separated in *Aeronautes*. Proposed race *dinellii* from Jujuy (NW Argentina) now incorporated into nominate race. Three subspecies currently recognized.

Subspecies and Distribution.

A. a. parvulus (Berlepsch & Stolzmann, 1892) - W Andes of Peru to extreme N Chile.

A. a. peruvianus (Chapman, 1919) - E Andes of Peru.

A. a. andecolus (d'Orbigny & Lafresnaye, 1837) - C Bolivia to W Argentina (Río Negro).



Descriptive notes. 14 cm. Medium-sized swift with broad inner wing, sharply pointed outer wing and long, deeply forked tail; black upperparts broken by narrow white trailing edge to secondaries, white rump band and white collar; largely white/off-white below on face, throat and underparts, with buff-mottled flanks and ventral area. Race *parvulus* slightly smaller than nominate and very contrastingly plumaged; *peruvianus* smaller than nominate with shorter and more shallowly forked tail; lacks buff tints to white plumage and has darker undertail-coverts and more interrupted collar.

Habitat. Main habitats defined as arid montane scrub and semi-humid or humid montane scrub. Typically over semi-arid mountainous areas, often bushy or with scattered cacti and more rarely over forested slopes, at 340-3900 m (2500-3550 m in Peru and Bolivia, 2000-2500 m in southernmost areas of range). Has been recorded above 4100 m in Peru.

Food and Feeding. Gregarious and highly mobile forager; associates with wintering *C. pelagica*. **Breeding.** Observed entering hole in road cutting where young were being fed, early Dec, N Tarapacá, Chile. Recorded nesting in holes in steep rock-faces, but nest form not recorded.

Movements. Resident. May move as a result of snowstorms at high altitude.

Status and Conservation. Not globally threatened. Common throughout range, except N Chile where uncommon and irregular at Arica, Camarones Gorge and Chusmisa in mountains of Tarapacá. Local and irregular in parts of Argentina.

Bibliography. Araya & Chester (1993), Bond & Meyer de Schauensee (1943), Canevari *et al.* (1991), Chapman (1919), Fjeldsá (1991), Fjeldsá & Krabbe (1990), González & Málaga (1997), Hughes (1988), Johnson (1967), Koepeke (1970), Krabbe *et al.* (1996), Narosky & Yzurieta (1993), Neller (1993), Nore *et al.* (1983), de la Peña (1982, 1994), Plenge (1974), Remsen & Traylor (1989), Remsen, Traylor & Parkes (1986), Stotz *et al.* (1996), Vuilleumier (1969), Wetmore (1926), Zimmer (1953b).

Genus TACHORNIS Gosse, 1847

69. Antillean Palm-swift

Tachornis phoenicobia

French: Martinet petit-rolé **German:** Kubasegler **Spanish:** Vencejillo Antillano
Other common names: Palm Swift(?)

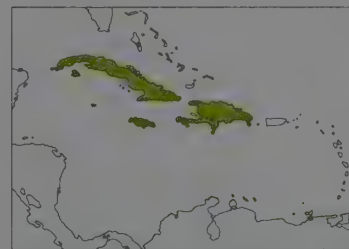
Taxonomy. *Tachornis phenicobia* Gosse, 1847, Jamaica.

Formerly placed alone in present genus. Two subspecies recognized.

Subspecies and Distribution.

T. p. iradii (Lembeye, 1850) - Cuba and I of Pines.

T. p. phoenicobia Gosse, 1847 - Jamaica; Hispaniola and nearby islands of Saona, Beata and Vache.



Descriptive notes. 9-10 cm. Small swift with large, obviously forked tail; black-brown upperparts broken by large white rump band with dark central stripe; white throat and central belly patch on otherwise brown underparts. Race *iradii* larger with deeper tail-fork, sootier upperparts and paler flanks and face.

Habitat. Main habitats defined as low, seasonally wet grassland and second-growth scrub. Mainly a lowland species, though can be recorded in mountains; collected at 450 m at Bombardopolis, Haiti. Always closely associated with royal palms (*Roystonea*), often close to human habitation, even in large cities. In

Port-au-Prince, Haiti, occurs around gardens with palms.

Food and Feeding. Encountered in small groups, occasionally with hirundines and other swifts. Observed entering a tannery to feed on flies inside low, open sheds.

Breeding. Seen entering clusters of dead palm fronds in May; believed to be feeding young in early Apr. Breeds colonially in palms. Nest is a globular construction of soft materials agglutinated with saliva, with nest cup at base. Clutch 3-5. No other information.

Movements. Resident, with vagrancy to Florida Keys and Puerto Rico suggesting some dispersal. **Status and Conservation.** Not globally threatened. Locally common in suitable habitat on all islands within its range. Occupation of man-made habitats such as large cities, e.g. Santo Domingo, suggests species is relatively adaptable and therefore secure.

Bibliography. Anon. (1998a), Barbour (1943), Bond (1956a, 1985), Dod (1987), Downer & Sutton (1990), Gundlach (1873), Kepler (1971), Lembeye (1850), Raffaele *et al.* (1998), Ridgway (1911), Stotz *et al.* (1996), Wetmore & Lincoln (1933), Wetmore & Swales (1931).

70. Pygmy Swift

Tachornis furcata

French: Martinet pygmée **German:** Däumlingssegler **Spanish:** Vencejillo Venezolano

Taxonomy. *Micropanyptila furcata* Sutton, 1928, Guachi, Zulia, Venezuela.

Previously placed in monospecific genus *Micropanyptila*; alternatively, on occasion in *Reinarda*, with *T. squamata*. Two subspecies recognized.

Subspecies and Distribution.

T. f. furcata (Sutton, 1928) - NE Colombia and NW Venezuela.

T. f. nigrodorsalis (Aveledo & Pons, 1952) - W Venezuela.



Descriptive notes. 10 cm. Tiny swift with long thin wings and long, deeply forked tail; uniformly brown upperparts; whitish throat, separated from whitish mid-belly by brown breast band with rest of underparts mid-brown. Race *nigrodorsalis* has blacker upperparts and whiter throat.

Habitat. Main habitats defined as tropical lowland evergreen forest, secondary forest and second-growth scrub. Habitats include primary and secondary forest, cultivated land and open areas with scattered trees, though must contain palms on which species depends for nest-sites.

Food and Feeding. Forages in small, highly active flocks.

Breeding. Pair collected at nest-site in late Jul, Catatumbo lowlands, Colombia. Noted to have similar nest structure to better-studied *T. phenicobia*, with similar dependency on palms.

Movements. Believed resident.

Status and Conservation. Not globally threatened. Restricted-range species: present in Caribbean Colombia and Venezuela EBA. Tiny range and small numbers of sites for which species is known suggest that population studies are urgently required.

Bibliography. Aveledo & Pons (1952), Bond (1956b), Hilty & Brown (1986), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Olrog (1968), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Sutton (1928).

71. Fork-tailed Palm-swift

Tachornis squamata

French: Martinet claudia **German:** Gabelschwanzsegler **Spanish:** Vencejillo Tijereta

Other common names: Neotropical Palm-swift, Fork-tailed Swift

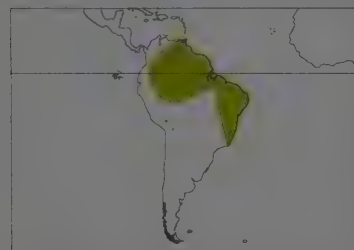
Taxonomy. *Cypselus squamatus* Cassin, 1853, Guyana.

Previously placed in genus *Reinarda*, alone or with *T. furcata*. Two subspecies recognized.

Subspecies and Distribution.

T. s. semota (Riley, 1933) - E Ecuador and NE Peru through E Colombia and NW Brazil to S & E Venezuela; possibly also N Bolivia.

T. s. squamata (Cassin, 1853) - the Guianas and Trinidad to C & E Brazil.



Descriptive notes. 13 cm; 12 g. Smallish swift with very long, deeply forked tail and long thin wings; black-brown upperparts; large white throat separated from white mid-belly by thin brown breast band; underparts otherwise brown. Race *semota* generally much darker with less feather fringing than nominate.

Habitat. Main habitats defined as palm forest, river-edge forest, low, seasonally wet grassland and second-growth scrub. Recorded from Amapá, N Brazil, over Amazonian upland savanna. Depends on buriti (*Mauritia*) palms for nest-sites, whether in an urban setting (often in good numbers in city parks), open landscapes

such as *llanos*, or forest clearings. Habitat survey in Villavieciencia area, Colombia, showed reliance on morichales biome, species being absent from all 8 other habitat types. Also around *Bactris* palms in Ecuador. Occurs to 1000 m but typically much lower, 200-1000 m on E slope of Ecuadorian Andes.

Food and Feeding. Not particularly gregarious, occurring in flocks of up to 10, and just as likely to be seen with Blue-and-white Swallow (*Notiochelidon cyanoleuca*) as with other swift species. Feeds at very low levels or just over canopy, and in lower strata of mixed swift flocks.

Breeding. In Trinidad breeds Apr-Jun; in Colombia fledgling collected late Feb near Leticia and male in breeding condition collected Vaupés, May; in Mato Grosso, Brazil, breeding behaviour recorded late Sept to Nov. Solitary. Requires buriti palm (*Mauritia*) leaves, which, on withering, crack at base to hang down at trunk; nest a J-shaped pouch 13 cm long, inner walls mainly down-lined, outer copiously feathered and rather disorderly, adhered with saliva at top and curving away from leaf, leaving entrance 30 mm across at base to egg trough, latter sited in middle of leaf some 16 cm from crack; nest wall 5 mm, 20 mm below egg trough; outer wall of trough 60-70 mm, inner wall 35 mm, depth 15 mm. 3 eggs, possibly secured to egg-shelf using saliva; incubation period 21 days.

Movements. Resident. May migrate in parts of Brazil, as absent from Borba (Rio Madeira), Mar-Nov. **Status and Conservation.** Not globally threatened. Locally common throughout range within morichales habitat. Common at Limoncocha, E Ecuador, and across Venezuelan and Colombian *llanos*. Relatively abundant in some urban areas, such as towns and cities of N Venezuela.

Bibliography. Duhs (1992), ffrench (1991), Friedmann (1948), Friedmann & Smith (1950), Gilliard (1941), Haverschmidt & Mees (1994), Herklots (1961), Hilty & Brown (1986), Marín (1993), Marín *et al.* (1992), McKay (1980), Meyer de Schauensee & Phelps (1978), Paz y Miño (1989), Pearson (1975), Remsen & Traylor (1989), Riley (1933), Schubart *et al.* (1965), Sick (1948a, 1993, 1997), da Silva *et al.* (1997), Snyder (1966), Stotz *et al.* (1996), Thomas (1990), Willis & Oniki (1993), Zimmer (1953b).

Genus *PANYPTILA* Cabanis, 1847

72. Great Swallow-tailed Swift

Panyptila sanctihieronymi

French: Martinet de San Geronimo **Spanish:** Vencejo Tijereta Grande

German: Großer Schwalbensegler

Other common names: Geronimo Swift

Taxonomy. *Panyptila sancti-hieronymi* Salvin, 1863, San Gerónimo, Vera Paz, Guatemala. Monotypic.

Distribution. S Mexico (Nayarit and Jalisco S to Chiapas), C Guatemala and S Honduras.



Descriptive notes. 18-20 cm; 50 g. Large swift with long thin wings and long, very deeply forked tail; black upperhead, white collar contiguous with large white throat, and black upperparts with white trailing edge to remiges; underparts black apart from white throat and rear flank patches.

Habitat. Main habitats defined as montane evergreen forest, pine forest, secondary forest and arid montane scrub. Mainly over montane habitats, 1200-1500 m in Mexico, 600-2000 m in Guatemala, and usually above 1000 m in Honduras, but recorded from lowlands of La Selva, Costa Rica, and to 500 m in valleys of

Honduras, when sometimes over human settlements. Typically over wild and rocky terrain.

Food and Feeding. 2 stomachs contained large numbers of winged termites and single pentatomid bugs (*Solubea pugnax*). One of least gregarious apodids. Often seen foraging at high elevation and at great speed.

Breeding. Very large tube-like nest, 660 x 150 mm, adhered along length, consisting of felt-like plant material agglutinated with saliva, with feathers attached to outside. As well as basal entrance, false entrance sited on tube side.

Movements. Generally considered resident, though series of Costa Rican and Nicaraguan records in Sept-Nov and Mar-Apr and movements in lowlands of NW Mexico close to sea-level during Dec-Jan suggest some degree of dispersal.

Status and Conservation. Not globally threatened. Uncommon to fairly common in Mexico and Guatemala; considered common in Honduras. Only recorded from Mexico for first time as recently as 1944, and there are still relatively few published records.

Bibliography. Álvarez del Toro (1952), Anon. (1998a), Binford (1989), Carr & Dickinson (1951), Griscom (1932a), Hernández-Baños *et al.* (1995), Howell & Webb (1994, 1995a), Land (1970), Monroe (1968), Ridgway (1911), Rowley (1984), Salvin (1863), Schaldach (1963), Selander (1955), Sick (1958), Stiles & Skutch (1989), Stotz *et al.* (1996).

73. Lesser Swallow-tailed Swift

Panyptila cayennensis

French: Martinet de Cayenne

German: Kleiner Schwalbensegler

Spanish: Vencejo Tijereta Chico

Other common names: Cayenne Swift

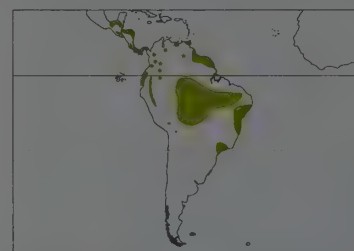
Taxonomy. *Hirundo cayennensis* J. F. Gmelin, 1789, Cayenne.

Separation into races may prove to be unjustified. Two subspecies currently recognized.

Subspecies and Distribution.

P. c. veraecrucis R. T. Moore, 1947 - E Mexico (Veracruz) to N Honduras.

P. c. cayennensis (J. F. Gmelin, 1789) - S Honduras S through Central America, with scattered distribution in W Colombia, Ecuador, Peru, NE Bolivia, Brazil, Venezuela, Trinidad and the Guianas.



Descriptive notes. 13 cm; 18 g. Medium-sized swift, black with white collar, throat and rear flank patches. Structure and plumage remarkably similar to much larger *P. sanctihieronymi*, but more grey-brown in collar area than latter; also shorter-winged (average nominate 119 mm and *veraecrucis* 126-8 mm, *P. sanctihieronymi* 188 mm). Race *veraecrucis* larger than nominate.

Habitat. Main habitats defined as tropical lowland evergreen forest and secondary forest. Mostly lowlands and foothills, to 1000 m in Mexico, 1500 m in Guatemala, 300 m in Honduras, 800 and 1000 m in Costa Rica on

Caribbean and Pacific slopes respectively, 1400 m in Colombia, 1000 m in Venezuela, and 1500 m in Ecuador where mainly below 900 m, with broader altitudinal range on Andean W slope (300-1500 m) than on E (200-600 m). Occurs over a variety of habitats, rarer in more arid areas, clearings and edges of primary or secondary forest, cultivated areas, over human habitations and rivers.

Food and Feeding. Occurs in mixed groups with *Chaetura* and *Cypseloides*, but generally less gregarious than other apodids, not typically in flocks of over 6. Feeds in lower strata of mixed flocks with *Cypseloides* or *Streptoprocne*, but in their absence occupies higher levels than other swifts.

Breeding. Recorded Costa Rica Jan-Jun, Panama Mar-Aug, and Caldas, Colombia, Apr and Dec. In Brazil occupied nests found in Mato Grosso in Feb and in Pará Jun-Sept, and nestlings in Rio de Janeiro in Nov. Solitary. Recorded nesting under eaves, against walls of occupied houses, inside deserted buildings and large forest trees. Two nest types: either sock-shaped, fixed by sole to branch, with entrance a narrow sleeve hanging from sole, or long sleeve attached for whole length to trunk or wall; both consist of plant down with felt-like structure, feathers frequently adhered to outside, agglutinated with saliva; dimensions range from 240 x 90 mm and 355 x 75 mm to 480 x 165 mm; entrance typically 10-50 mm wide. Clutch 2-3. Both adults roost in nest throughout year.

Movements. Resident. Recorded as rare vagrant during Nov over secondary-scrub habitat 30 km S of Caracas, Venezuela, in 18 years, suggesting only small degree of dispersal.

Status and Conservation. Not globally threatened. Local and uncommon, to locally fairly common in optimum habitat, such as Hill Bank, N Belize. Fairly common to uncommon in Central American range; perhaps less abundant in South America, where rare to uncommon in Ecuador, and uncommon in Venezuela and Colombia. Usually encountered in small numbers only.

Bibliography. Arnold (1966), Beebe (1949), Boesman (1998), Carr & Dickinson (1951), Edwards (1959), Graves & Zusi (1990b), Greenway (1934), Haverschmidt (1954a, 1971), Haverschmidt & Mees (1994), Herklots (1961), Hilty (1977), Hilty & Brown (1986), Howell & Webb (1995a), Kiff (1975), Kirwan & Sharpe (1999), Marín (1993), Marín *et al.* (1992), Meyer de Schauensee & Phelps (1978), Monroe (1968), Moore (1947b), Munves (1975), Pacheco & Whitney (1995), Parker & Remsen (1987), Parker *et al.* (1991), Peres & Whittaker (1991), Ridgely & Gwynne (1989), Ridgway (1911), Rogers (1939a), Salaman & Gandy (1994), Schulenberg & Parker (1981), Sick (1947, 1958, 1993, 1997), Slud (1964), Snyder (1966), Stiles & Skutch (1989), Stotz *et al.* (1996), Teixeira *et al.* (1988), Thomas (1993), Valley & Whitman (1997), Weimore (1968a), Zimmer (1953b).

Genus *CYPSIURUS* Lesson, 1843

74. African Palm-swift

Cypsiurus parvus

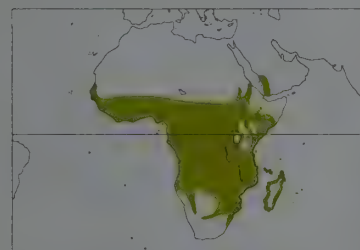
French: Martinet des palmes **German:** Palmensegler **Spanish:** Vencejo Palmero Africano
Other common names: Palm Swift (when joined with *C. balasiensis*); Madagascar Palm-swift (*gracilis*)

Taxonomy. *Cypselus parvus* Lichtenstein, 1823, Nubia.

Forms superspecies with *C. balasiensis*, with which previously considered conspecific. Race *gracilis* (with *griveaudi*) may prove to be a distinct species. Eight subspecies currently recognized.

Subspecies and Distribution.

- C. p. parvus* (Lichtenstein, 1823) - Senegambia to Ethiopia, S to S Sudan; also SW Arabia.
- C. p. brachypterus* (Reichenow, 1903) - Sierra Leone to NE Zaire, S to Angola; islands in Gulf of Guinea.
- C. p. myochrous* (Reichenow, 1886) - S Sudan to NE South Africa (Transvaal), preferring highlands.
- C. p. laemostigma* (Reichenow, 1905) - coastal lowlands from S Somalia to Mozambique.
- C. p. hyphaenes* Brooke, 1972 - N Namibia and N Botswana.
- C. p. celer* Clancey, 1983 - Mozambique to Natal.
- C. p. griveaudi* Benson, 1960 - Comoro Is.
- C. p. gracilis* (Sharpe, 1871) - Madagascar.



Descriptive notes. 16 cm; 10-18 g. Very small swift with very long, very deeply forked tail, usually appearing needle-thin when tightly closed, and long, very thin wings. Pale grey-brown upperparts, with head and particularly wings appearing darker; underparts uniform and very pale with some streaking on throat; underwing-coverts darker than underbody. Male has whiter throat than female. Juvenile has more rufous fringes than fresh adult and lacks long emarginate outer rectrices. Race *laemostigma* darker, throat more mottled, and smaller; *myochrous* as latter with more greenish gloss; *brachypterus* darker than preceding races, throat

as nominate; *hyphaenes* paler than nominate, with least marked throat; *celer* similar to *myochrous*, though warmer tone with restricted pale fringing and fine streaking restricted to upper throat; *griveaudi* very dark with heavy streaking on throat and upper breast; *gracilis* darker than African races, with heavily streaked throat, juvenile with deeper tail-fork than juveniles of other races.

Habitat. Always contains palms, particularly fan palms, on which depends largely for nest-sites, though sympathetically constructed bridges also now used to some extent. Suitable palm species found from arid to rainforest zones. In Saudi Arabia occupies areas of Tihamah coastal plains where doum palm (*Hyphaene thebaica*) present. In Liberia, where infrequent within forest blocks, uses coconut (*Cocos*) and more locally *Borassus*, but not oil palm (*Elaeis*). Similarly choosy in S Africa, where pinnate palms generally shunned, whereas large dense population thrives in *Hyphaene* palm belt in N Botswana and Owambo. Typically occurs in lowlands, to 1100 m in Madagascar and rarely to 1700 m on Comoros; mainly below 1400 m in Kenya, though breeding locally to 1800 m. On Comoros prefers lowlands, where occurs through coconut belt without reaching forest edge areas.

Food and Feeding. Recorded contents from 32 stomachs: flies 17, ants 6, termites 4, beetles 3, c. 100 winged termites 1, and many small ants 1. Noted in groups of 4-8 at Kariba, Zimbabwe, with Lesser Striped Swallows (*Hirundo abyssinica*), Wire-tailed Swallows (*H. smithii*) and *Neafraus boehmi* in lowest of 3 feeding levels, below 20 m. This stratification apparent only when several species present; fed at other levels when alone or with just 1 other species. Believed to be most crepuscular swift in South Africa, where feeding period overlaps that of microchiropteran bats.

Breeding. Over much of range breeds year-round, though mainly in warmer months. Laying dates: May-Aug, Senegambia; Sept-Oct and Jun, Liberia; May, Burkina Faso; Nov-Jun, N Nigeria; Sept-Oct, Principe I; Apr-May, Jul-Aug and Nov-Jan, Cameroon; Mar, Central African Republic; Nov-Sept, Sudan; Jan and perhaps Jun, Ethiopia; Mar, May-Oct and Dec-Jan, majority Aug-Sept, Zambia; Mar, Jun-Jul, Sept-Oct and Dec-Jan, Malawi; year-round, of 288 nests 9% Apr-Jun, 37% Dec-Jan, Zimbabwe; Jun-Nov, South Africa; Sept-Nov, Madagascar; eggs and juvenile recorded late Sept, Comoro Is. Solitary or colonial. Typically nests in palms but man-made structures also used, as are leaves of *Dracaena*; recorded nesting in *Eucalyptus*, where nest placed in leaf clusters, in area lacking indigenous palms. Nest consists primarily of seed-down, more when cotton floss used, and typically soft feathers, agglutinated with saliva and sited on upper side of palm frond, or next to trunk between base of 2 fronds on *Washingtonia* palms; nest cup protrudes 4-15 mm away from back wall of nest and 45-120 mm along frond, and is 45-55 mm wide. Copulates only at nest. Typically 2 eggs, though 1 and 3 recorded, and 3 on average in Madagascar, with first egg laid 10 days after nest-building started; both sexes incubate, at night with partner resting on nest pad or close by, with frequent change-overs; rigid incubation posture with abdomen pressed against eggs, eyes remaining open during day; great variation in incubation percentage time noted, not clearly correlated with climatic variables; similar extremes noted in brooding, also by both sexes; incubation not always apparent in rain; average incubation period in Tanzania 20 days; at hatching, adult presses young tightly to nest; within hours of hatching young very restless, even while being brooded; from day 4 vertical crawling away from flange; little brooding from day 9; only 1 young fed on each visit, mean feeding rates per chick per 200 minutes 3.8 for brood of 1, 2.75 for brood of 2; average fledging period 31 and 33 days for broods of 1 and 2, respectively. In Tanzania, of 35 eggs laid, 23 hatched and 6 young fledged; average breeding success 17%, with 0.3-1.9 young fledged per breeding attempt.

Movements. Resident over much of range, but present only during summer in most southerly breeding area in South Africa. Extralimital records probably indicate range expansion. Two unidentified *Cypsiurus* at Al Ain in 1996 were first United Arab Emirates record.

Status and Conservation. Not globally threatened. Common to locally abundant. In Kenya commonest on coastal strip and far less apparent in W. Locally common in Tihamah coastal plains of Saudi Arabia. Race *gracilis* very common in Madagascar and *griveaudi* common on Comoros. Scarcest in areas of recent colonization. Use of exotic *Washingtonia* palm, native to SW USA, considered a major cause in recent range expansion, which is continuing in S Africa and seems to have begun in 1930's. However, westward expansion of African elephant (*Loxodonta africana*) into Okavango, coupled with frequent fires, may threaten species locally as a result of palm reduction.

Bibliography. Ade (1975), Anon. (1997a), Ash & Miskell (1998), Atkinson, Dutton *et al.* (1994), Bannerman (1953), Barlow *et al.* (1997), Beaman & Madge (1998), Benson (1960), Benson & Benson (1977), Benson, Brooke

et al. (1971), Benson, Colebrook-Robjent & Williams (1976-1977), Berruti & Brooke (1985), Brooke (1963, 1968, 1971), 1972b, 1980), Brooke & Avery (1992), Bunning (1987), Butcher (1975), Cave & Macdonald (1955), Chantler (1993), Chapin (1939), Cheke & Walsh (1996), Christy (1998), Christy & Clarke (1994), Clancey (1983), Coetsee (1981), Collins (1965), Cramp (1985), Donnelly (1974, 1982), Donnelly & Howells (1982), Dowsett & Forbes-Watson (1993), Driessens (1994), Elgood *et al.* (1994), Evans (1994), Field (1998), Friedmann (1930), Fry *et al.* (1988), Gatter (1997), van Gelder (1996), Ginn *et al.* (1989), Goodman *et al.* (1989), Gore (1990), Grimes (1987), Harrison *et al.* (1997), Hofmeyr (1994), Jennings (1995), Jones & Tye (1988), Langrand (1995), Lewis (1990), Lewis & Pomeroy (1989), Lippens & Wille (1976), Louette (1981, 1988a), Louette *et al.* (1988), Mackworth-Praed & Grant (1957, 1962, 1970), Maclean (1993), Markus (1963), Martin *et al.* (1988), Milon *et al.* (1973), Moreau (1941), Mortimer (1975a, 1975b), de Naurois (1994b), van Niekerk (1992), Nikolaus (1987), Pakenham (1979), Penry (1994), Pérez del Val (1996), Pinto (1983), Porter, Christensen & Schiermacker-Hansen (1996), Rahmani *et al.* (1994), Rand (1936), van Reenen (1968), Safford & Duckworth (1990), Sala (1998), Sargeant (1992a), Short *et al.* (1990), Snow (1978), Snow & Perrins (1998), Stagg (1985), Steyn & Brooke (1971), Thompson & Buisson (1988), Vernon (1991a), Ward *et al.* (1984), Whyte (1982), Wilkes (1928), Zimmerman, D.A. *et al.* (1996).

75. Asian Palm-swift

Cypsiurus balasiensis

French: Martinet batassia **German:** Bengalsegler **Spanish:** Vencejo Palmero Asiático

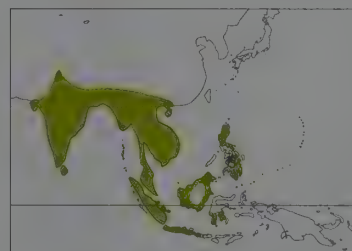
Taxonomy. *Cypselus Balasiensis* J. E. Gray, 1829, India.

Forms superspecies with *C. parvus*, with which previously considered conspecific. Sulawesi in process of being colonized from S, by either *infumatus* or *bartelsorum*. Species name often erroneously listed as *batasiensis*. Four subspecies recognized.

Subspecies and Distribution.

- C. b. balasiensis* (J. E. Gray, 1829) - Indian Subcontinent W of Assam hills.
- C. b. infumatus* (P. L. Slater, 1865) - Assam hills to Indochina, Malay Peninsula, Sumatra and Borneo.
- C. b. bartelsorum* Brooke, 1972 - Java and Bali.
- C. b. pallidior* McGregor, 1905 - N & E Philippines.

Birds that have recently colonized S & SE Sulawesi may be either *infumatus* or *bartelsorum*.



Descriptive notes. 13 cm. Very small swift with long thin wings and long, deeply forked tail shorter than that of adult *C. parvus* and lacking streamer-like emarginated outermost rectrices. Mid-grey upperparts, slightly paler rump; pale grey underparts, underwing-coverts appearing darker, with unstreaked throat. Race *infumatus* darker, especially on rump and glossy black-brown rectrices and outer remiges, with shorter tail and shallower tail-fork; *bartelsorum* lacks fringing in juvenile and has lightly streaked throat; *pallidior* paler than *infumatus*, rump quite uniform with mantle, tail shorter and less forked than in *bartelsorum*.

Habitat. Primary dependence on fan palms (*Livistona*, *Borassus*, *Corypha*, *Arecia*) but in some areas thatched roofs used as nesting and roosting sites. Forages adjacent to sites, especially over mangroves and paddy, where palms prevalent. Although mainly a lowland species, as are fan palms, recorded to 1000 m in India and Sri Lanka, 1500 m in Java and Myanmar, and 1320 m on Sulawesi. Common even in city parks. Rarest in dense forest, though clearings and edges utilized. Resident over scrub and dry deciduous forest in Mudumalai Wildlife Sanctuary, SW India.

Food and Feeding. Hemiptera, Coleoptera and Hymenoptera recorded. Detailed Malaysian study of nestling diet (both faeces and bolus) found Coleoptera, Isoptera, Hymenoptera, Diptera, Homoptera and Ephemeroptera, with predominance of flying ants, termites and beetles. Mean open-country foraging height 13.3 m. Frequent in mixed flocks with other swifts and hirundines. Forages particularly actively in evening. Very gregarious; recorded in flocks of up to 1000, though 40 or below more frequent. In S India large numbers feeding on alate rice earhead bugs (*Leptocoris acuta*) were most active in early morning, numbers decreasing from 10:00 onwards as temperature increased.

Breeding. Virtually year-round with local variation of peak, mainly Mar-Aug in lowlands and Apr-Jun in hills, India; Dec to early Jul, Malay Peninsula; recorded Oct and Apr, Sumatra, but probably also year-round. Solitary. Typically nests on palm fronds, but where these are scarce will nest in eaves of thatched roofs. Nest is flimsy half-cup of seed-down (Malaysian study revealed sole use of either *Ceiba pentandra* or *Phragmites communis*) agglutinated with saliva, c. 10 mm deep x 40-50 mm wide, supporting apron extending over 50 mm above nest; feathers also used, under 5% in Malaysian study, to lesser extent than in *C. parvus*; eggs not glued to nest with saliva as in *C. parvus*, perhaps due to deeper, more secure, egg chamber and more continuous incubating habits during stormy weather; sited under palm leaves or near midrib frond of older leaves which hang down almost vertically; nest in Malaysia completed in 8 days. Clutch 2 eggs, though 1 and 3 recorded, mean 1.93 in Malaysia; both sexes incubate for c. 78% of time, though incubation continuous during inclement weather; mean feeding interval 45 minutes, shortest early morning and longest midday; adults incubate in vertical position, mean period for last egg 18 days; in 2-egg clutches 1-day interval between eggs hatching; young initially blind and naked, primary feathers in pin on day 6 and split on day 14, eyes opening on day 7 and movement in nest vicinity on day 14; young cling to apron when nest becomes too full; mean nestling period 28.5 days. Overall egg success 38%. Two clutches recorded in 46% of nests, with interval between first brood fledging and start of second clutch 8-26 days.

Movements. Resident.

Status and Conservation. Not globally threatened. Common to locally abundant. Least common where fan palms at lowest density. May be absent where palm crowns vigorously cut back, perhaps due to loss of roosting sites. Apparent range expansion in parts of Wallacea: first recorded in 1978 in S & SE Sulawesi, where now quite common; single record from Talaud Is of 3 birds in Sept 1995, presumably referring to birds of race *pallidior*; report of many birds at Kapan, Timor, in Jan 1990 would, if confirmed, imply a major range extension.

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PLATE 43

inches 6
cm 15



Genus *TACHYMARPTIS* Roberts, 1922

76. Alpine Swift

Tachymarptis melba

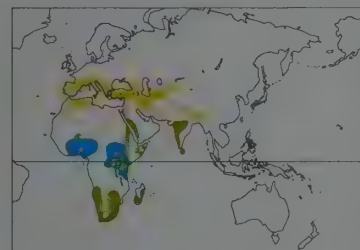
French: Martinet à ventre blanc **German:** Alpensegler **Spanish:** Vencejo Real
Other common names: Ceylon White-bellied Swift (*bakeri*)

Taxonomy. *Hirundo Melba* Linnaeus, 1758, Gibraltar.

Genus *Tachymarptis* has commonly been merged into *Apus*, but nowadays increasingly separated; differs in feather lice, foot structure of nestling, large size and tendency towards white underparts. Race of Mali birds not yet established, but their isolation from other breeding populations suggests it could be an undescribed race. Proposed race *striatus* from Mt Kenya is synonym of *africanus*. Subspecies name *dorabatai* often misspelt *dorabatai*. Ten subspecies currently recognized.

Subspecies and Distribution.

T. m. melba (Linnaeus, 1758) - S Europe through Asia Minor to NW Iran; winters in W & E Africa.
T. m. tuneti (Tschusi, 1904) - C & E Morocco through Middle East and Iran (except NW) to SE Kazakhstan and W Pakistan; winters in W & E Africa.
T. m. archeri (Hartert, 1928) - Somalia, SW Arabia N to Dead Sea depression.
T. m. maximus (Ogilvie-Grant, 1907) - Mt Ruwenzori (Uganda/Zaire).
T. m. africanus (Temminck, 1815) - E & S Africa and SW Angola; S birds winter in E Africa.
T. m. marjoriae (Bradfield, 1935) - Namibia to NW Cape (South Africa).
T. m. willsi (Hartert, 1896) - Madagascar.
T. m. nubifuga (Koelz, 1954) - Himalayas; winters in C India.
T. m. dorabatai (Abdulali, 1965) - W peninsular India.
T. m. bakeri (Hartert, 1928) - Sri Lanka.
Also resident (subspecies unknown) in Mali.



Descriptive notes. 20-22 cm; 104 g. Very large swift with broad wings and shallowly forked tail relatively shorter than in *Apus*; olive-brown upperparts lacking prominent saddle, outer wing appearing blacker; underparts with white throat and highly distinctive large oval white patch encircled by olive-brown breast band, flanks and undertail-coverts. Races *tuneti* and *marjoriae* paler, with grey-brown plumage; *archeri* averages paler than *tuneti*, with shorter wings; *maximus* largest race, with very dark, blackish plumage; *africanus* and *nubifuga* smaller than nominate, with blacker plumage, smaller throat patch and blacker shaft-streaks

on white areas; *willsi* and *bakeri* both smaller, with darker plumage and broader and narrower breast bands respectively; *dorabatai* has broader breast band and shorter wings than *nubifuga* and separated from *bakeri* by its lighter plumage and broader breast band.

Habitat. A polytypic species occurring over a wide range of habitats and foraging over vast areas. In W Palearctic in temperate and Mediterranean zones, typically in mountains but occasionally in lowlands. In remainder of sub-Saharan Africa and S Asia occurs from sub-desert steppe to equatorial mountains. Typically breeds below 1500 m, sometimes to 2200-2300 m. May breed above 4000 m on high mountains in Kenya and forage to 3700 m in Himalayas. Seen entering probable nesting sites at 2100 m on Madagascar.

Food and Feeding. Swiss food balls for nestlings averaged 219 prey items, ranging from 11 to 626, mean weight 2.53 g, mainly Hymenoptera, Coleoptera and spiders. Seventeen food balls comprised 308 flies, 200 beetles, 125 aphids, 94 wasps, 21 spiders, 16 cicadas (Cicadidae), 15 lacewings (Neuroptera), 2 ants and 2 butterflies. Other Swiss prey species were wood wasps (*Sirex gigas*), drone honeybees (*Apis mellifera*) and dragonflies. In Africa grasshoppers and winged termites also taken. A single bug species comprised the vast majority of prey in a series of stomachs from Zaire. In South Africa believed to be a significant predator in spring around commercial apiaries during cool, windy, overcast weather. Usually forages higher than most other swifts, e.g. in highest feeding level, 30-40 m, at Kariba, Zimbabwe, but will feed at low levels, especially during inclement weather. Has been observed taking cicadas flushed by a human. Will feed at night either where lights attract insects or even in total darkness as recorded in Saudi Arabia.

Breeding. Season Mar-Jun, Israel: laying Morocco Apr-May, Samarkand from early May, C Europe mid-late May or in bad weather as late as early Jun, Zimbabwe Aug, South Africa Sept-Jan; nestlings being fed Caucasus early Jul, Kugitang Mts (Central Asia) mid-Jul; fledging from nest Dagestan, Caucasus, early Jul; breeding behaviour noted late Sept and mid-Oct, Madagascar. Colonial, mixed colonies with *Apus barbatus* frequent; colonies may last for hundreds of years. Monogamous, with bond of at least 11 years recorded. Uses ledges or holes in cliff-faces or tall man-made structures; nest-site used in successive years by pair. Nest saucer-shaped, consists of downy feathers from many species, and swift primaries, tightly bound with dried plant matter and saliva. 125 x 130 mm, mean height 39 mm on level surface and 49 mm on angled surface in Europe, typically with central depression averaging 28 mm on horizontal surfaces; nest bowls on flatter surfaces average deeper; in Africa those attached to vertical rock-face externally 90 x 110 mm, inner bowl 100 x 110 x 20 mm, those wedged in vertical crack 80 mm wide measured 70 mm deep, internal bowl 80 x 110 x 20 mm. Copulation by nest or in air. Typically 3 eggs (1-4); incubation 17-23 days with nest duties shared by both sexes; whole clutch hatches within 24 hours; average 10 feeds daily; nestling period 53-66 days. In Switzerland, 94% of eggs hatch successfully and 78-98% of broods fledge; overall breeding success 70%, with average of 1.8-2.4 young fledged per breeding effort. Breeds first at 2-3 years, less frequently at 1 year.

Movements. Nominate race, *tuneti*, *nubifuga* and S African populations of *africanus* migratory. Migrants at high altitude, and often movements observed only when poor weather forces birds down. Palearctic breeding populations leave Sept to mid-Oct, returning from mid-Feb, later farther N, e.g. late Mar to early Apr to Switzerland. Main migration through Belen Pass, S Turkey, Oct-Nov, where in smaller flocks than *Apus apus* and mainly in single-species groups. At Bosphorus migratory picture unclear, as large Istanbul population embarks on early-morning feeding movements, but peak autumn

passage early Sept. In Israel, autumn passage late May to mid-Dec, peaking Sept-Oct; spring passage mid-Jan to mid-Jun, peaking mid-Feb to late Mar; huge migration noted over West Bank in mid-Mar 1987, when 10,000 flew N in 15 minutes, only 50-100 m above ground. In Natal performs altitudinal migration from 1500-2400 m to below 900 m. Recorded once along Egyptian Nile in Feb, in Arab Gulf states on 3 occasions Nov-Jan; small numbers, mostly *tuneti*, winter Israel, mainly in desert areas; S African populations partially migratory: breeding areas occupied Aug-May, with migration noted May-Jun and Aug-Oct through Zimbabwe, Mar-Apr and Aug-Oct Malawi, and probably Apr and Sept Botswana. Other races in Africa and India show some non-breeding dispersal, thought to be linked to monsoon. Large numbers recorded Feb-Apr in N Liberia of unknown migratory provenance, since Palearctic and African migrants believed to occur in that country and breeding cannot be ruled out. Annual overshooting migrant to British Is and C & N Europe; 3 Caribbean records.

Status and Conservation. Not globally threatened. Locally fairly common to common throughout much of range. Locally abundant in some areas, e.g. Turkey, Central Asian republics and parts of Africa where resident; perhaps increasing in S Africa, where increasingly using buildings as nest-sites. One colony lost in late 1960's as a result of dam construction. Locally abundant also in Indian Subcontinent. Swiss population has fluctuated, with minimum of 1250 pairs annually during 1970-1974, at least 61% utilizing buildings; severe weather in 1974 caused crash to maximum of 320 pairs during 1975-1978, subsequently increased to 1200-1300 pairs in 1994. Similar fluctuations reported from Bulgaria (decline of large colony from 300-500 pairs to c. 100 pairs) and Italy (desertion of colonies due to poor spring weather). Range expansion, with some regional increases, within stable European population. Swiss population has increased since 1990 as purpose-built nestboxes have been sited on many tall buildings. Population estimates in 1997: Europe 44,614-62,482 breeding pairs, Turkey 10,000-200,000 pairs.

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77. Mottled Swift

Tachymarptis aequatorialis

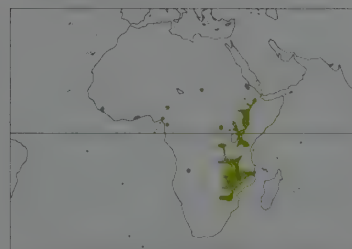
French: Martinet marbré **German:** Schuppensegler **Spanish:** Vencejo Ecuatorial

Taxonomy. *Cypselus aequatorialis* von Müller, 1851, Ethiopia.

Genus *Tachymarptis* has commonly been merged into *Apus*, but nowadays increasingly separated; differs in feather lice, foot structure of nestling, large size and tendency towards white underparts. It has been suggested that resemblance to *Apus bradfieldi* may be more than superficial, hinting at closer alliance between these forms, which were formerly considered conspecific. Races proposed for birds from W slope Mt Ruwenzori (*schubotzi*) and NW Cameroon (*bamendae*) not distinct from nominate race and included within it. Includes "*Apus reichenowi*". Four subspecies currently recognized.

Subspecies and Distribution.

T. a. lowei (Bannerman, 1920) - Sierra Leone to Nigeria.
T. a. furensis (Lynes, 1920) - Darfur (W Sudan).
T. a. aequatorialis (von Müller, 1851) - Eritrea and Ethiopia S to Mozambique and E Zimbabwe; also SW Angola and NW Cameroon (*Bamenda*).
T. a. gelidus (Brooke, 1967) - SW Zimbabwe.



Descriptive notes. 23 cm; male 92.5 g, female 96 g. Very large swift with long, broad wings and long, moderately forked tail; blackish mantle contrasts slightly with head and distinctly with rump; inner wing paler than blackish outer wing; blackish underparts heavily barred, with indistinct pale throat patch. Race *gelidus* similar but smaller, with whiter throat, greyer upperparts and blacker barring on breast; *furensis* may average larger than nominate, with greyer upperparts, more extensive throat patch and pale belly patch caused by narrow barring in that area; *lowei* intermediate between nominate and *furensis* below, with upperparts similar to *gelidus*.

Habitat. Breeding restricted to granite highlands, where recorded up to 3000 m, occasionally higher, although widely scattered range encompasses both arid and equatorial mountain ranges. Forages widely and encountered over adjoining habitats, often at great height. Where sympatric with *T. melba*, generally breeds at lower elevations.

Food and Feeding. Recorded prey comprises ants, including *Crematogaster* (*Acrocnolia*), ichneumonid flies (Ichneumonidae) with other Hymenoptera, flies, termites and frequently beetles. In low-level foraging, feeds mainly on honeybees (*Apis mellifera*). Gregarious, typically in flocks of 20-40 and often with other swift species, especially *T. melba*, but occasionally in very large flocks of up to 1000.

Breeding. Laying dates: Ghana Jun and Oct, Nigeria possibly Nov-Jun, Ethiopia Jul, Kenya Feb-Mar, probably with 2 breeding seasons at Njorowa Gorge coinciding with rainy seasons, Tanzania Jun-Jul and Nov, Malawi Aug-Sept, Zambia Oct, Zimbabwe Jun and Aug-Nov; *furensis* have enlarged gonads Jun and small gonads Feb-Mar; specimen of *lowei* taken in breeding condition late

On following pages: 78. Alexander's Swift (*Apus alexandri*); 79. Common Swift (*Apus apus*); 80. Plain Swift (*Apus unicolor*); 81. Nyanza Swift (*Apus niansae*); 82. Pallid Swift (*Apus pallidus*); 83. African Swift (*Apus barbatus*); 84. Forbes-Watson's Swift (*Apus berliozi*); 85. Bradfield's Swift (*Apus bradfieldi*); 86. Pacific Swift (*Apus pacificus*); 87. Dark-rumped Swift (*Apus acuticauda*); 88. Little Swift (*Apus affinis*); 89. House Swift (*Apus nipalensis*); 90. Horus Swift (*Apus horus*); 91. White-rumped Swift (*Apus caffer*); 92. Bates's Swift (*Apus batesi*).

Apr. Typically colonial; males allegedly outnumber females by 50% and, though monogamous, this may indicate co-operative breeding; colonies poorly synchronized. Nest built over several weeks in vertical, or close to vertical, crack in rock-face, under rock overhang or 2-3 m above cave floor in vertical cleft; at least 6 m clear airspace needed for approach unless in cave; dry granite rock favoured. Sturdy, bracket-shaped nest consists of wind-dispersed seeds and feathers with leaves agglutinated with saliva, adhered to vertical surface or on 45° overhang, measuring 80-87 mm wide, 60-65 mm front to back and 25-48 mm deep. Clutch 1-2; both sexes incubate.

Movements. Poorly understood. Non-breeding dispersal implied by wide scatter of records away from breeding areas and by common occurrence of non-breeding (presumed) nominate race during summer in W Sudan and as far W as Chad. Will follow storms, where presumably benefits from updraughts. Rare visitor to W Liberia on 4 occasions, late Feb to early Apr. Vagrant to Hexrivier Pass, Cape Town, some 1000 km from limit of breeding range.

Status and Conservation. Not globally threatened. Common to abundant in much of range. Very localized within W African range, though large numbers recorded from Wase Rock, Nigeria, e.g. 2500 roosting in Mar 1997. Numerical status of Angolan or Cameroon populations unknown.

Bibliography. Anon. (1997a), Balança & de Visscher (1993, 1997), Bannerman (1933, 1953), Bednall (1958, 1959, 1963), Benson (1952), Benson & Benson (1977), Benson *et al.* (1971), Brooke (1967, 1968, 1969a, 1969c, 1971b, 1971, 1973a), Cave & Macdonald (1955), Cheke & Walsh (1996), Cooke (1965), Devise (1992), Dowsett (1976, 1989a), Dowsett & Dowsett-Lemaire (1978a), Duckworth *et al.* (1992), Elgoud *et al.* (1994), Field (1998), Fry *et al.* (1988), Gatter (1997), Ginn *et al.* (1989), Grimes (1974, 1987), Harrison *et al.* (1997), Karcher (1989), Lippens & Wille (1976), Louette (1981), Lynes (1925), Maclean (1993), Masterson (1945, 1946), Nikolaus (1987), Osborne (1975), Osborne & Osborne (1978), Pinto (1983), Short *et al.* (1990), Snow (1978), Steyn (1966b), Zimmerman, D.A. *et al.* (1996).

Genus *APUS* Scopoli, 1777

78. Alexander's Swift

Apus alexandri

French: Martinet du Cap-Vert **German:** Alexandersegler **Spanish:** Vencejo de Cabo Verde
Other common names: Cape Verde Swift

Taxonomy. *Apus unicolor alexandri* Hartert, 1901, São Nicolau, Cape Verde Islands. Affinities unclear. Formerly considered conspecific with *A. unicolor*; recently suggested to be more closely related to *A. pallidus*, *A. barbatus* or *A. niansae*, although these proposals appear to be based mainly on speculation. Only known eggs, described in 1898, were considered unique amongst Apodiformes in being speckled reddish brown; a second clutch reported in 1986, however, consisted of pure white eggs, as in other Apodiformes, suggesting that the first set were probably misidentified; implications drawn from the first eggs have greatly confused the issue of relationships. Monotypic.

Distribution. Cape Verde Is. where occurs throughout (except Santa Luzia), including small islet of Raso, but thought to breed only on Santiago, Fogo, Brava, Santo Antão and São Nicolau.



Descriptive notes. 13 cm. Small, short-winged swift with relatively shallow tail-fork and distinctive fluttering flight; darkest black-brown on outer wing, wing-coverts, tail and mantle, with paler brown forehead and rump, the latter producing a prominent saddle; underparts paler still with broad, diffuse, off-white throat-patch; rest of underparts darker away from throat, pale brown lightly barred darker.

Habitat. Occurs over all habitats on small island range, foraging from sea-level up to peaks of highest mountains, e.g. 2830 m on Fogo. Breeds up to 1600 m.

Food and Feeding. Forages alone or in parties of up to 30.

Breeding. Noted visiting nest-sites Aug-Sept; eggs collected early Apr and mid-Nov; breeding suspected Jan-Mar, early Jun and Aug-Sept on Santiago, Feb on São Nicolau and Aug-Sept on Brava. Nests in cliff fissures and in houses. 2 eggs, plain white.

Movements. Resident, though foraging birds, or non-breeders, occur on E islands and São Vicente. Occasional absence noted from some islands, e.g. São Vicente and Santo Antão in Jan-Feb 1966.

Status and Conservation. Not globally threatened. Restricted-range species; present in Cape Verde Islands EBA. Common, with largest numbers on Fogo and Brava. Population not accurately censused, but certainly numbers in the thousands. Early records indicate abundance on São Nicolau.

Bibliography. Alexander (1898), Bannerman (1953), Bannerman & Bannerman (1966, 1968), Beaman & Madge (1998), Boume (1955, 1957), Brooke (1971b, 1971i), Chantler (1993), Cramp (1985), Dowsett & Dowsett-Lemaire (1993), Driessens (1994), Hazevoet (1995), Hazevoet *et al.* (1996), Lack (1956a), de Nairois (1986, 1994a), Noeske & Plütze (1994), Norrevang & Hartog (1984), Snow & Perrins (1998), Stattersfield *et al.* (1998), White (1960).

79. Common Swift

Apus apus

French: Martinet noir **German:** Mauerssegler **Spanish:** Vencejo Común
Other common names: (Eurasian/European/Northern) Swift

Taxonomy. *Hirundo Apus* Linnaeus, 1758, Sweden.

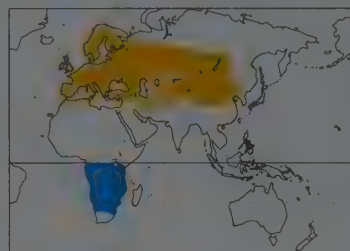
Forms superspecies with *A. unicolor* and *A. niansae*; has been considered conspecific with both, and also with *A. barbatus*. Birds breeding in SW Asia have been separated in race *marwitzi*, but not widely accepted. Israeli population somewhat intermediate between nominate race and *pekinensis*. Two subspecies normally recognized.

Subspecies and Distribution.

A. a. apus (Linnaeus, 1758) - W Palearctic E to L Baikal, SE towards Iran; winters mainly from Zaire and Tanzania S to Zimbabwe and Mozambique.

A. a. pekinensis (Swinhoe, 1870) - Iran E through W Himalayas to Mongolia and N China; winters primarily in Namibia and Botswana.

Descriptive notes. 16-17 cm; 36-52 g. Large rakish swift with long, deeply forked tail and sharply pointed wings; black-brown mantle, outer wing, lesser coverts, tail, crown and underparts beneath



small off-white throat patch; slightly paler inner wing, greater coverts of underwing, forehead and rump; contrast between paler and darker tracts varies individually and temporally, fresh feathers being blacker with narrow white fringes. Juvenile very black, with little contrast between tracts; white fringes most apparent on forehead, which can show as small white patch, and larger, more defined white throat-patch. Race *pekinensis* has paler forehead and shows greater contrast in wing.

Habitat. Wide range of habitats from arid steppe and desert on S & E boundaries, temperate and Mediterranean zones N into boreal zone; also

over all sub-Saharan habitats. Recorded from sea-level to high altitude. Abundance in Britain and Ireland seemingly correlates with climate; commonest in relatively warm and dry S & E, becoming scarcer to N & W, where cooler, wetter and windier weather reduces insect abundance. In Israel primarily in Mediterranean climatic zone, with only small numbers in semi-desert areas. Race *pekinensis* occurs in Himalayas at 1500-3300 m, foraging to 4000 m, and recorded migrating at 5700 m in Ladakh. **Food and Feeding.** Prey up to 12 mm taken, with stinging insects avoided. Over 500 prey species noted in European diet. German study analysed 11,384 insects and 17 spiders: 53% were Hemiptera, 26% Coleoptera, 10% Diptera and 3% Lepidoptera and Neuroptera.

Breeding. Season: Mar-Jun, Israel; probably May-Jun, Pakistan and Kashmir; mid-May to late Jul Britain and Ireland, and a week earlier and later in Switzerland and Fennoscandia respectively; in Turkmenistan, nest-building at Kopet-Dag in Apr, completed nest Kyzylcha-kala in early May, clutches completed in Ashkhabad from late Apr; laying NW Africa in May, and Russia early-mid Jun. Colonial, though solitary nests not infrequent; separate nests, typically over 1 m apart. Site prospected and chosen by male; initially female greeted with hostile display, though allopreening occurs when she submits by lifting head to expose throat patch; copulation on wing and at nest. Nests mainly in buildings, but in remote parts of range also in tree hollows and rock crevices. Nest cup constructed of small pieces of vegetable matter and feathers, agglutinated with saliva, measuring 125 × 110 mm, internal diameter 45 mm. Clutch 1-4, averaging 2 in N Africa but typically more in Europe; both sexes share nesting duties equally; incubation, initiated by laying of last egg, occurs in equal periods of c. 2 hours, more intensive when weather poor; period 19-5 days; brooding continuous in first week, discontinuous from second, with young unattended during inclement weather; down that grows from day 13 is extensive by day 17, being fully replaced by day 30; feeding rate depends on weather, average 10 food balls daily in Gibraltar; 2 young share food ball until large enough to swallow one whole by day 14; nestlings restless from 2-3 weeks, with wing exercises and allopreening; average fledging period 42.5 days (wide range of 37-56 days due to weather conditions), self-initiated fledging after sunset or prior to 08:00. Average breeding success 58-65%, with mean 1.3-1.7 young fledging per breeding effort.

Movements. Long-distance migrant. Present at SW Palearctic sites from mid-Mar, arriving later farther N; main arrival N Europe early May, with migration persisting to early Jun. Main spring and autumn passage in Egypt late Mar to mid-May and mid-Aug to mid-Oct; records in late Jan to early Feb could indicate local wintering or early migration. Spring migration of nominate race through Israel mid-Jan to mid-Jun, peaking Apr-May; passage S throughout country mid-May to mid-Nov; in spring *pekinensis* moves mainly in Mar-Apr, occurring primarily in E in autumn. Leaves N Europe from late Jul, mainly Aug, very rare from Nov. Autumn movement over W Turkish migration watchpoints peaks mid-late Aug. Present on African wintering grounds from Sept. Broad-front autumn migration from Europe on SSW bearing, returning by generally more E route. Race *pekinensis* departs South Africa by early Mar, nominate race leaving somewhat earlier, late Jan to early Feb. Winters in small numbers N of Sahara, e.g. Cape Verde Is, with records Aug-Jun, possibly in Egypt among flocks of *A. pallidus* along Nile, in Israel and Arab Gulf states. Vagrant to many oceanic archipelagos, including Pribilof Is off Alaska (1 record, Jun) and Prince Edward Is in S Indian Ocean.

Status and Conservation. Not globally threatened. Declines apparent in some areas of Europe at least, where breeding population recently reported to have decreased in 12 countries. In Britain and Ireland, census work during 1968-1972 revealed an estimated 100,000 pairs; between then and 1989-1990 there is no evidence of significant population change, and it is believed that if previous figure is correct there are c. 80,000 and c. 20,000 pairs in Britain and Ireland respectively. Population estimates (breeding pairs) in 1997: Europe 3,973,943-4,872,619, Russia 1,000,000-5,000,000 and Turkey 50,000-500,000. Has recently colonized Canary Is, on Gran Canaria and probably Tenerife.

Bibliography. Ali & Ripley (1983), August (1992), Beaman & Madge (1998), Becker (1982), Bernis (1988), Bowen (1977a), Bretagnolle (1993), Brichetti & Caffi (1994), Brooke (1975a, 1975b), Brooke & Taylor (1967), Casement (1963), Chantler (1993), Chursch (1956), Clancey (1981, 1981b), Colombo & Galeotti (1993), Courdesse & Gory (1995), Cramp (1985), Cucco *et al.* (1993), Dolnik & Kinzhewskaja (1980), Driessens (1994), Duan Wenrui *et al.* (1989), Farina (1980, 1988), Flath (1980), Fry (1988c), Fry *et al.* (1988), Gary (1987), Gérardet (1960), Gladwin & Nau (1964), Godel (1962), Goodman *et al.* (1989), Gorgass (1985), Gory (1987, 1988, 1991a, 1991b, 1992a, 1992b, 1993, 1994a, 1994b, 1997), Gory & Jeantet (1986a, 1986b), Grobe (1983, 1985, 1986), Gross (1998), Günther & Hellmann (1993), Gustafson, Lindkvist *et al.* (1977), Gustafson, Magnusson *et al.* (1985), Hagemeijer & Blair (1997), Hao Jigang (1985), Harrison *et al.* (1997), Herremans & Herremans-Tonnoeyr (1994), Holmgren (1986, 1987, 1993), Hurrell (1955), Ingram (1972), Inskip & Inskip (1991), Ji Jiayi *et al.* (1988), Kainady (1977), Kaiser (1984, 1992, 1997), Keskipaikka (1973), Kolonen & Peiponen (1991), Koskimies (1947, 1948, 1950), Kroymann (1991), Lacey (1910), Lack (1955, 1956a, 1956c, 1956d, 1956e, 1958a, 1958b, 1958d, 1964), Lack & Lack (1951b, 1952, 1954), Lack & Owen (1955), Lavkumar (1958), Lawley (1979), Lehtikoinen & Lindstrom (1988), Leys (1988), Lockley (1971), Lotem (1998), Lowe (1962), Luleyeva (1993), Malacarne *et al.* (1989), Martins (1997), Martins & Wright (1993a, 1993b, 1993c), Mayaud (1951), Morrison (1946), Nicolau-Guillaumet & Williams (1982), Nothum *et al.* (1989), O'Connor (1979), Offringa (1996), Paterson (1966), Pavelka & Korytar (1990), Pellantova (1975, 1981), Perrins (1964, 1971), Randi & Boano (1993), Reese (1997), Reuter *et al.* (1980), Roberts (1991), Rodríguez-Tejedor (1980), Rogacheva (1992), de Roo (1966b, 1967), Schiegrer (1962), Shirhai (1996), Simpson (1967), Snow & Perrins (1998), Stadler & Schmitt (1917), Svårdson (1951), Thomson & Douglas-Home (1993), Thomson *et al.* (1996), Tickle (1966), Tigges (1994, 1995), Turek (1956), Veysey (1965), Vizyova & Janiga (1986, 1987), Wallace (1961), Wang Xiangting (1958), Weinauer (1947, 1956, 1975, 1977), Wynne-Edwards (1964), Xu Chuanming (1985), Yakobi (1980), Zhao Zhengjie (1995), Zimmerman, D.A. *et al.* (1996).

80. Plain Swift

Apus unicolor

French: Martinet unicolore **German:** Einfarbsegler **Spanish:** Vencejo Unicolor

Taxonomy. *Cypselus unicolor* Jardine, 1830, Madeira.

Forms superspecies with *A. apus* and *A. niansae*; has been considered conspecific with both, and also with *A. barbatus*. In past, considered conspecific with *A. alexandri*. *Shouedenapus myoptilus poensis* formerly treated as race of present species. Monotypic.

Distribution. Canary Is and Madeira; possibly breeds in Morocco.



Descriptive notes. 14-15 cm. Medium-sized swift with even more streamlined outline than *A. apus*, long, deeply forked tail and long thin wings; black-brown outer wing, tail and mantle, with paler, dark brown forehead, rump and underparts beneath indistinct mottled throat-patch. Like *A. apus*, plumage contrast, shade and fringing vary temporally, but appearance averages more barred beneath.

Habitat. Throughout established range, and tentative Moroccan range where frequents sea cliffs, never found far from sea. Occurs over all habitats in Canaries from sea-level to 2500 m; especially common in deep coastal gulleys.

On Madeira from sea-level to highest summit, Pico Ruivo, breeding on rocky islets.

Food and Feeding. Typically insectivorous, but no detailed study. Forms large groups in winter around favoured feeding sites.

Breeding. Season Mar-Aug. Colonial. Nests in variety of natural sites, such as caves and cliffs, where suitable rock niches occur, or under tiles or in holes in man-made structures. Saucer-shaped nest constructed largely from downy seed cases, mainly from *Compositae*, with other plant matter or man-made items less frequently incorporated, agglutinated with saliva with occasional feathers adhered to surface, measuring 100-120 mm across with central depression 10-20 mm wide. 2 eggs; both sexes thought to incubate. Frequently double-brooded.

Movements. Numbers reduced in winter on Canary Is; migrants probably winter mainly in NW Africa, as winter records from Mauritania and N Morocco.

Status and Conservation. Not globally threatened. Restricted-range species; present in Madeira and Canary Islands EBA. Common and apparently stable. Madeira is believed to have 1000-2000 breeding pairs according to 1991 census.

Bibliography. Bannerman (1963), Bannerman & Bannerman (1965), Beaman (1994), Beaman & Madge (1998), Brooke (1971b), Chantler (1993), Cramp (1985), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Driessens (1994), Dunn (1994), Emmerson (1979), Etchecopar & Hùe (1964), Fry *et al.* (1988), Hagemeijer & Blair (1997), Herroelen (1994), Hollom *et al.* (1988), Lack (1956a), Lorenzo & González (1993), Martín (1987), Meininger *et al.* (1990), Moreno (1988), Reese (1997), Rodríguez (1988), Smith (1968), Snow & Perrins (1998), Stattersfield *et al.* (1998), Zehner (1980).

81. Nyanza Swift

Apus niansae

French: Martinet du Nyanza

German: Braunsegler

Spanish: Vencejo de Nyanza

Other common names: Brown Swift

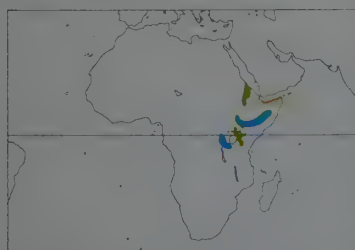
Taxonomy. *Cypselus Niansae* Reichenow, 1887, Kagehi, Lake Victoria.

Forms superspecies with *A. apus* and *A. unicolor*; has been considered conspecific with both, and also with *A. barbatus*. Race *somalicus* formerly considered to belong to *A. pallidus*. Two subspecies currently recognized.

Subspecies and Distribution.

A. n. niansae (Reichenow, 1887) - Eritrea, W Ethiopia, E Uganda, W Kenya and N Tanzania; winter records from N & NE Zaire, NW Tanzania, Somalia, Ethiopia and Kenya.

A. n. somalicus (S. R. Clarke, 1919) - N Somalia and adjacent Ethiopia; some birds winter in Kenya.



Descriptive notes. 15 cm; male 32 g, female 33 g. Medium-sized swift with small head, rakish wings, comparatively short and shallowly forked tail with relatively blunt rectrices; blackest on mantle, outer wing and smallest coverts, showing extreme contrast with pale brown inner wing and greater coverts; brown head and rump less notably paler than inner wing; brown underparts with pale throat. Race *somalicus* averages paler and smaller with more distinct pale throat-patch.

Habitat. Although can be encountered in lowlands, typically occurs in highland areas and associated habitats, gorges, cliff-faces and also human settlements. Arid character of much of

habitat suggests necessity of accessible, relatively wet area as source of abundant food.

Food and Feeding. Prey items recorded: ants 14, flies 7, beetles 2, bugs 1, bees 1 and termites 1. Most active in crepuscular period, though feeds throughout day close to active breeding colonies. Large colony at Hell's Gate, Kenya, forages in daytime high over nearby Lake Naivasha outside breeding season, leaving in early morning and returning at dusk. Gregarious, often associating with other swift species.

Breeding. Laying dates: Eritrea Apr-May, C Ethiopian plateau Apr-Aug, Addis Ababa May-Sept, Kenya Sept; *somalicus* thought to breed in May. Colonial: Addis Ababa colony in a building fluctuated between 20 and 195 pairs over 5 years, though only 10-50 pairs nested at any one time, while at another colony 4-9 nesting attempts per season recorded. Nests in crevices on cliff-faces or in gorges, or in similar niches in buildings. Shallow cup of feathers and grasses agglutinated with saliva, with grass base and possibly some mud incorporated as well as concrete fragments, up to 120 mm wide externally, with internal cup 85-110 mm across and 25-30 mm deep; use of mud seen as tactic to close small space, on to which feathers and sometimes hat bones can be added. Aerial copulation. Clutch 1-3; both sexes incubate, 2-3 periods each during day, one or other on eggs at night with mate beside nest; incubation minimum 19 days; fledging 41 days. Gonad growth suggests first breeding 1 year after hatching.

Movements. In N Somalia present late Mar to late Sept, probably only partially migratory. Addis Ababa colonies present in both rainy seasons, Feb-Apr and Jun-Sept, though this population also only partially migratory. Individuals believed to be wintering birds recorded from Kenya. Other populations resident.

Status and Conservation. Not globally threatened. Generally common to abundant throughout the Rift Valley Highlands. Huge colony at Hell's Gate National Park, Naivasha, Kenya, numbers 10,000's of individuals. Apparently adapts well to man-modified areas, and is common in Addis Ababa.

Bibliography. Archer & Godman (1937-1961), Ash & Miskell (1983b, 1988), Britton (1980), Brooke (1969c, 1970a, 1971b), Brown & Britton (1980), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Duckworth *et al.* (1992), Dyson (1972), Fry (1988e), Fry *et al.* (1988), Grant & Mackworth-Praed (1937), Lewis & Pomeroy (1989), Lippens & Wille (1976), Schwab (1979), Short *et al.* (1990), Smith (1955a, 1955b, 1957), Snow (1978), van Someren (1922), Urban (1984), Urban & Brown (1971), White (1953), Zimmerman, D.A. *et al.* (1996).

82. Pallid Swift

Apus pallidus

French: Martinet pâle

German: Fahlsegler

Spanish: Vencejo Pálido

Other common names: Mouse-coloured Swift

Taxonomy. *Cypselus pallidus* Shelley, 1870, Egypt.

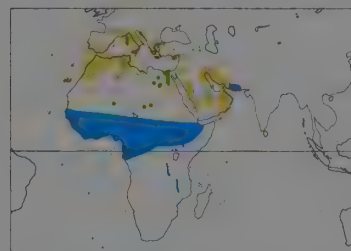
Forms superspecies with *A. barbatus*, *A. berliozii* and *A. bradfieldi*. *A. niansae somalicus* formerly placed in present species. Three subspecies currently recognized.

Subspecies and Distribution.

A. p. brehmorum Hartert, 1901 - W Palearctic from Portugal E to Turkey (except Dalmatian coast), and from Morocco to NW Egypt, including Canary Is and Madeira; winters in Sahel.

A. p. illyricus Tschusi, 1907 - Dalmatian coast and possibly E Italian coast; winters in Sahel.

A. p. pallidus (Shelley, 1870) - Banc d'Arguin through Sahara to Middle East and Pakistan; migratory populations winter in Sahel, with limited wintering coastal Pakistan.



Descriptive notes. 16 cm; 42 g. Large, bulky swift with relatively broad blunt wing-tips, short, fairly shallowly forked tail, broad head and body. Brown, with white throat-patch. Race *brehmorum* larger and darker than nominate, with black-brown outer wing and saddle, smallest wing-coverts minimally paler, greater coverts (including greater primary coverts) and inner wing distinctly paler, entire head, lower back and rump greyer brown and forehead pale grey-brown (pronounced saddle effect), and underparts olive-brown with large, indistinct, triangular pale grey throat-patch contiguous with forehead patch and sometimes strikingly

barred in appearance; *illyricus* slightly larger and darker, with more distinct throat-patch as a result.

Habitat. Throughout much of range associated with coastal sites, especially islets, but occurs in continental zone in C Sahara. Typically found around cliff-faces and gorges, though in many parts of range also in urban areas, where commonly breeds. Forages over many habitats, to 1750 m on Cyprus and 1200 m on Canary Is. Breeds to 1250 m in mountainous plateau of S Italy and to 2700 m in SW Bulgaria. Approximately 42% of Bulgarian population breeds at 1200-1600 m around ski resorts in coniferous woodland, with 38% at 200-500 m in rural and suburban areas.

Food and Feeding. At Gibraltar, 1293 prey items comprised Hymenoptera 56%, Hemiptera 25%, Diptera 12%, Coleoptera 5%, Lepidoptera 1%, and others, including Odonata and spiders, 1%. Small beetles and small flies, including mosquitoes, recorded in Tunisia, and flying ants in Algeria. Gregarious, often associating with other swift species.

Breeding. Laying dates: Israel, Mar-May; Morocco and Tunisia, Mar-Jul, with first clutch from Apr and second clutches beginning late Jul, with last fledging mid-Oct; Gibraltar, first clutch from mid-Apr, peaking late May, with second clutches from late Jul and last fledging mid-Oct. Colonial: 48% of colonies on Gibraltar with fewer than 10 pairs, largest 60 pairs; 3-300 m between colonies; lower level of mate and nest-site fidelity than in *A. apus*. Nests in variety of sites, e.g. caves, cliff-faces, niches, eaves, under tiles, holes in palms, and on Gibraltar forcibly vacated fresh nests of House Martins (*Delichon urbica*); 70% of nests under eaves, 15% in holes in stonework, 7% under gutters and 7% on cliffs. Round nest of straw and feathers agglutinated and adhered to substrate with saliva, 80-100 x 100-120 mm across and 40-50 mm deep, with central depression 25 mm deep, occupied 4-7 days before laying starts. Copulation in flight after soliciting by gliding with raised wings, often after long pursuit. Typically 2 or 3 eggs (1-4 recorded), on Gibraltar first clutches mean 2.9 eggs, second clutches 1.9; both sexes incubate, period 21.5 days; hatching asynchronous; chicks brooded day and night initially, with up to 4 feeding visits per hour; fledging period 46.5 days. Double-brooded. On Gibraltar, fledging rate 53% for first-clutch eggs and 30% for second-clutch eggs.

Movements. Southernmost and some Middle Eastern breeders resident; additional wintering in S Spain and as far N as France recorded, but generally otherwise a medium-distance migrant. Present in France early Apr to mid-Nov, Gibraltar and Morocco late Feb to Oct and Canaries Jan-Sept. Migrates through NW Africa late Feb to early May and Aug-Nov. Spring migration through Eilat, Israel, peaks late Feb to mid-Apr, with autumn migration late May to late Sept, mainly Jun-Jul. Very common passage migrant in Djibouti. Present on Gambian wintering grounds Oct-Dec, as late as Apr in reduced numbers, but in some central N African areas some present all year. Rare visitor to W Liberia late Feb to early Apr. Vagrant S to South Africa. Wintering recorded in India E to Sind.

Status and Conservation. Not globally threatened. Abundant in some areas, including much of N Africa and W Mediterranean. Huge count of 8000-12,000 birds made from an area of cliffs in SE Mali. Locally uncommon in many peripheral areas such as Canaries, Turkey and S France. In 1976, French population thought to be 100-1000 pairs; marked increase in population and range since first mainland breeding in 1950. Single colony of 8000 birds at Sevilla, Spain, in 1986. Stable or possibly slightly increasing European population, with greatest abundance in Spain, Portugal, extreme S France, Corsica, Sardinia, Croatia and Greece; slight decline in Gibraltar and Greece, with Albanian range declining. Population estimates (breeding pairs) in 1997: Europe 21,202-32,893 and Turkey 10-1000. Large colonies in Israel, with 2000 pairs at Har Sedom.

Bibliography. Affre & Affre (1967), Ali & Ripley (1983), Anon. (1988b), Aspinall (1996), Bannerman (1953), Barlow *et al.* (1997), Beaman & Madge (1998), Benson *et al.* (1971), Bernis (1988), Bigot *et al.* (1984), Blankert (1980a), Boano (1979), Boano & Cucco (1989), Boano *et al.* (1993), Bretagnolle *et al.* (1995), Brichetti *et al.* (1988), Brooke (1968, 1969a, 1970a), Burges (1983), Calvert (1984), Casement (1963), Castan (1955), Chantler (1990, 1993), Cheke & Walsh (1996), Colombo & Galeotti (1993), Cramp (1985), Cuadrado *et al.* (1985), Cucco (1992), Cucco & Malacarne (1987, 1995, 1996a, 1996b, 1996c), Cucco, Bryant & Malacarne (1993), Cucco, Malacarne, Orecchia & Boano (1991, 1992), Cucco, Malacarne & Poncino (1994), Diaz, Asensio & Telleria (1996), Driessens (1994), Dudley *et al.* (1996), Dunn & Wilson (1985), Duquet & Frémont (1995), Elgood *et al.* (1994), Evans (1994), Finlayson (1979), Finlayson & Tomlinson (1993), Flaxman (1987), Fry *et al.* (1988), Gatter (1997), Gélouet (1961), Gimpel *et al.* (1986), Goodman & Watson (1983), Goodman *et al.* (1989), Gore (1990), Gory (1995), Gory *et al.* (1995), Grimes (1987), Grimmett *et al.* (1998), Hagemeijer & Blair (1997), Hanby (1985), Harvey (1981a, 1981b), Hazevoet (1995), Heim de Balsac (1949/50), Hirschfeld (1995), Iankov (1991), Jennings (1995), Kainady (1976), Kennedy (1986), Kroymann & Kroymann (1991), Lack (1958c), Lack & Lack (1951a), Ladbroke & Smart (1984), Laferrère (1972, 1974), Lethaby (1987), Malacarne & Bertolo (1994), Malacarne & Cucco (1990, 1991, 1992), Malacarne, Cucco & Bertolo (1994), Malacarne, Cucco & Clemente (1987), Malacarne, Cucco & Orecchia (1992), Malacarne, Palomba *et al.* (1989), Mayaud (1951), Mazzotto *et al.* (1996), Mingozzi *et al.* (1988), Molteni (1964), Morgan (1990), Neubaur & Trettau (1959), O'Toole (1994), Ojalvo (1993), Palomeque *et al.* (1980), Penlop *et al.* (1997), Piacentini *et al.* (1996), Pulcher (1985), Purroy (1997), Randi & Boano (1993), Roberts (1991), Rodríguez de los Santos & Rubio (1986), Shirihi (1996), Short & Horne (1981), Smart (1984), Snow (1978), Snow & Perrins (1998), Telleria (1981), Thibault *et al.* (1987), Thiollay (1974), Thonnérieux (1987), Walbridge & Cade (1986), Wallace (1961), Wassink (1980), Welch & Welch (1984), Yeatman (1976).

83. African Swift

Apus barbatus

French: Martinet du Cap **German:** Kapsegler **Spanish:** Vencejo de El Cabo
Other common names: Black Swift(!), African Black Swift; Fernando Po Swift (*sladeniae*); Madagascar Swift (*balstoni*)

Taxonomy. *Cypselus barbatus* P. L. Sclater, 1865, Cape of Good Hope.

Forms superspecies with *A. pallidus*, *A. berliozi* and *A. bradfieldi*. Has been considered conspecific with *A. apus* and also with *A. unicolor* and *A. niansae*. Races *sladeniae* and *balstoni* (possibly with *mayottensis*) sometimes treated as two further distinct species. It has been suggested that if race *hollidayi* can remain a distinct breeding population despite presence of migratory nominate race during local breeding season, then it may prove to be a separate species. Current knowledge about taxonomic status of *glanvillei*, *sladeniae* and *serlei* to some extent compromised by scarcity of specimens; racial identity of population resident in N Liberia unknown, but may prove to be *sladeniae*; in contrast, *sladeniae* might even be applicable only to birds of Bioko. Nine subspecies recognized.

Subspecies and Distribution.

A. b. glanvillei Benson, 1967 - Sierra Leone.

A. b. sladeniae (Ogilvie-Grant, 1904) - SE Nigeria, W Cameroon (Mt Kupe), Bioko and W Angola; possibly this race in N Liberia.

A. b. serlei de Roo, 1970 - W Cameroon (Bamenda).

A. b. roehli Reichenow, 1906 - E Ethiopia, NE Uganda and Kenya to Malawi and E Zaire; also Sombo in NE Angola.

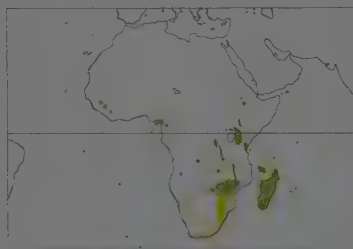
A. b. hollidayi Benson & Irwin, 1960 - Victoria Falls, on Zambia/Zimbabwe border.

A. b. oreobates Brooke, 1970 - Melsett to Mashonaland (Zimbabwe) and Mt Gorongosa (Mozambique).

A. b. barbatus (P. L. Sclater, 1865) - South Africa, and may occur W into mountainous areas of Namibia; wintering grounds unknown.

A. b. mayottensis (Nicoll, 1906) - Comoro Is.

A. b. balstoni (Bartlett, 1880) - Madagascar.



Descriptive notes. 16 cm; 42 g. Large, bulky swift, with broad blunt-tipped wings, short, shallowly forked tail and heavy body; black underparts with whitish throat-patch; black outer wing and saddle; notable inner wing contrast, and paler forehead and rump. Contrast between inner and outer wing less than in *A. niansae*. Race *glanvillei* slightly darker; *sladeniae* very dark, especially on throat, which lacks any paler feathers in some birds; *serlei* darker, lacking blue gloss on mantle and with underpart fringing more restricted; *roehli* smaller and darker; *hollidayi* paler with uniform wing-coverts; *balstoni* similar to *roehli*.

averaging darker with more uniform mantle, smallest coverts and outer wing; *mayottensis* slightly browner than *balstoni*.

Habitat. Primarily in moist mountains, typically breeding at 1600-2400 m, less often at 1000 m and below, and also over adjacent, even lowland habitats. Noted at 300-2150 m in Marojejy, Madagascar. Found over all habitats on Comoros. In S Cape and in Madagascar, breeds on sea cliffs.

Food and Feeding. Beetles, ants, termites and bees recorded; c. 12 beetles 8 mm long found in 1 stomach. Forages over forest canopy, and also at lower levels where forest more open with large trees. Gregarious, frequently in flocks up to 100, regularly with other swifts. Noted feeding lower than *A. caffer* or *Tachymarpis melba*. One seen feeding in middle feeding level, 20-30 m, at Kariba, Zimbabwe.

Breeding. Laying Malawi Aug-Sept, Zimbabwe Sept, South Africa Sept-Feb, Madagascar Nov-Mar; in E Africa breeding correlated with cool dry season, mid-year, or rainy seasons; possible *sladeniae* recorded in Liberia were visiting probable nest-site in crack in vertical granite dome, also used by Lesser Striped Swallows (*Hirundo abyssinica*). Red-rumped Swallows (*H. daurica*) and Rock Martins (*H. fuligula*), in late May. Typically colonial, recorded in mixed colony with *Tachymarpis melba*. In E Africa nests mainly in hollows in mature trees, especially cedars (*Juniperus procera*); favours niches in non-granite cliffs, including sea cliffs near Cape Town, in some cases within sea-spray zone, though possible tree-breeding recently recorded. Nest a shallow pad of grass, occasionally seed-down, and feathers, with untidy base and neat, sturdy, yet thin top; materials collected in flight. Clutch 1-2.

Movements. Nominate race present as breeder in South Africa Aug to mid-May, with presumed migration through Kariba, Zimbabwe, in May and Aug, while some probably overfly Botswana. However, wintering recorded from S Cape, Swaziland and Natal. It has been suggested that *balstoni* may be migratory to some extent, with decline in numbers noted in SW Madagascar Apr-Jul and on High Plateau Apr-Sept. Resident in other areas of range. In Natal, altitudinal migration from 1500-2400 m to below 900 m. Situation in Zimbabwe complex, with many "black" swifts present at Victoria Falls Nov-Apr, including small numbers of *hollidayi* and larger numbers of *A. apus*, but majority assumed to be migratory South African population of nominate race. W African race *sladeniae* may be only a vagrant to Bioko, while 2 possible *sladeniae* recorded from Principe in 1997.

Status and Conservation. Not globally threatened. Form *sladeniae* Data-deficient, known from only 10 records. All 3 W African races also known from only a small number of specimens. Locally abundant in South Africa and locally common in E Africa. In Kenya, locally common in W highlands. Restricted race *mayottensis* common in Comoros, where seen throughout; a group of 100 on Grand Comoro (Ngazidja) in early Aug 1981. Race *balstoni* widespread and common in Madagascar, with aggregations of several thousands recorded.

Bibliography. Anderson, M.D. (1994), Anon. (1995g, 1997a, 1998b), Bannerman (1953), Bannerman & Bates (1924), Basilio (1963), Benson (1960, 1967a), Benson & Benson (1977), Benson & Irwin (1960), Benson, Brooke *et al.* (1971), Benson, Colebrook-Robjent & Williams (1976-1977), Broekhuysen (1971), Brooke (1968, 1969a, 1970a, 1971b, 1972d, 1994), Chapin (1939), Cheke & Walsh (1996), Collar & Stuart (1985), Collar *et al.* (1994), Donnelly (1974), Dowsett & Dowsett-Lemaire (1993), Elglood *et al.* (1994), Field (1998), Fry (1988c), Fry *et al.* (1988), Gatter (1993, 1997), Good (1952), Harrison *et al.* (1997), Hockey *et al.* (1989), Hustler (1996), Johnson & Maclean (1994), Lack (1956a), Langrand (1995), Lewis & Pomeroy (1989), Louette (1988a), Maclean (1993), Martin, R. *et al.* (1985), Milon *et al.* (1973), Muller & Herremans (1995), Parker (1971, 1972), Penry (1994), Pérez del Val (1996), Pérez del Val *et al.* (1997), Pinto (1983), Rand (1936), Reichenow (1907), de Roo (1970), Safford & Duckworth (1990), Short *et al.* (1990), Snow (1978), Thompson & Buisson (1988), Traylor (1960), Zimmerman, D.A. *et al.* (1996).

84. Forbes-Watson's Swift

Apus berliozi

French: Martinet de Berliozi **German:** Sokotrasegler **Spanish:** Vencejo de Socotora

Other common names: Berliozi's/Watson's Swift

Taxonomy. *Apus pallidus berliozi* Ripley, 1965, Socotra.

Forms superspecies with *A. pallidus*, *A. barbatus* and *A. bradfieldi*. Birds breeding in SE Somalia (Hal Hambo) are apparently intermediate between nominate and race *benisoni*. Two subspecies recognized.

Subspecies and Distribution.

A. b. berliozi Ripley, 1965 - Socotra.

A. b. benisoni Brooke, 1969 - Somalia; winters S to coastal Kenya.



Descriptive notes. 16 cm; male 37-5 g, female 40 g. Plain brown, with forehead and lores intermediate in shade between *A. apus* and *A. pallidus*. Very like *A. pallidus* in structure and plumage, but slightly darker overall, with less distinct saddle and oily sheen on primaries, secondaries and median upperwing-coverts, and less contrast between inner wing and outer wing, latter particularly important relative to other resident plain *Apus*: slightly paler overall than *A. apus pекinensis*, with larger, whiter throat-patch and oily sheen on upper secondaries and median coverts, and separable in hand by longer average bill length (tomium

18-20 mm in *benisoni*, 16-18 mm in *A. a. pекinensis*) and apparently by P10 being longest (P9 generally longest in *pekinensis*). Race *benisoni* darker and browner than nominate, with more rounded throat-patch, less marked underparts and darker forehead.

Habitat. Generally found in arid landscapes. On Socotra seen over a wide range of habitats, even urban ones; in mountains occurs at 700-1200 m, favouring craggy areas. Coastal breeders nest in cliffs and caves, foraging over stabilized dunes. In Kenya, where non-breeding visitor, seen over coastal lowland forest.

Food and Feeding. Beetles, ants, grasshoppers, termites and bugs recorded. Typically forages in small numbers, c. 10, though flock of 200 recorded.

Breeding. Breeds at Hal Hambo, Somalia, Mar-Sept, or perhaps Dec, though this may be due to disturbance; completed by mid-May on Socotra. Colonial. Nests in holes in ceilings of sea-caves; saucer-shaped or pad-like nest 110-130 mm wide and 30-60 mm deep, sometimes lacking central depression, composed of dry seaweed (*Cymodocea*) agglutinated with saliva to a variety of materials, including sand, feathers, fishing line and plant matter. 2 eggs.

Movements. Race *benisoni* partial migrant, with some wintering on Indian Ocean coast as far S as Kenya, in coastal lowlands, where recorded Oct-Feb from Arabuko-Sokoke and Gede Forests S to Diani, Gazi and Shimba Hills. Otherwise resident. Unidentified *Apus* in Aden during Apr-Jul may prove to be this species.

Status and Conservation. Not globally threatened. Range very restricted. Common at main Socotran breeding site in Hajhir Mts, e.g. 300 recorded in survey, spring 1993. Range may be slightly more extensive than currently thought.

Bibliography. Ash & Miskell (1983b, 1998), Britton (1980), Brooke (1969b, 1969c, 1971b, 1972c), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Dymond (1966b), Evans (1994), Fry (1988c), Fry *et al.* (1988), Jennings (1995), Kirwan *et al.* (1996), Lewis & Pomeroy (1989), Porter, Christensen & Schiormacker-Hansen (1996), Porter, Dymond & Martins (1996), Ripley (1965), Ripley & Bond (1966), Short *et al.* (1990), Snow (1978), Zimmerman, D.A. *et al.* (1996).

85. Bradfield's Swift

Apus bradfieldi

French: Martinet de Bradfield **German:** Damarasegler **Spanish:** Vencejo de Namibia

Taxonomy. *Micropus bradfieldi* Roberts, 1926, Namibia.

Forms superspecies with *A. pallidus*, *A. barbatus* and *A. berliozi*. It has been suggested that resemblance to *Tachymarpis aequatorialis* may be more than superficial, hinting at closer alliance between these forms, which were formerly considered conspecific. Two subspecies recognized.

Subspecies and Distribution.

A. b. bradfieldi (Roberts, 1926) - SW Angola and Namibia.

A. b. deserticola Brooke, 1970 - N Cape (South Africa).



Descriptive notes. 18 cm; 42-5 g. Large swift with structure typical of *A. pallidus* group; relatively pale and lacking distinct saddle; black-brown outer wing and tail contrast with inner wing and paler brown upperparts; indistinct pale throat-patch on grey-brown, heavily patterned underparts. Race *deserticola* slightly darker-bodied, with resultant increase in throat-patch contrast.

Habitat. Occurs over a variety of arid habitats, including true desert and open savanna.

Food and Feeding. Insects, including honeybees (*Apis mellifera*) and termites. Latter particularly important, taken after emergence

precipitated by summer storms. In Namibia, noted resting on ground near hives while catching bees in flight, probably foraging for young at colony 24 km distant.

Breeding. Race *bradfieldi* probably breeds c. Aug-May (laying Apr, Namibia; nestlings Oct, Angola); *deserticola* recorded breeding in South Africa in Dec-Jan, Mar and May. Colonial. Nests in fissures in granite or basalt rocks, old buildings and disused mine workings, possibly also in dead palm fronds. Flat, cup-like nest of vegetable matter, including straw probably taken from nests of Pale-winged Starlings (*Onychognathus naboroupp*), and small feathers; 100 mm long, 105 mm wide and 35-55 mm deep, with central depression averaging 87 x 24 mm; adhered to angle of fissure with saliva. 2 eggs.

Movements. Mainly resident with some dispersal after breeding.

Status and Conservation. Not globally threatened. Commonest swift in C Namibia and generally common throughout range. Believed to have colonized E to Big Hole in Kimberley during 20th century. Formerly classified as South African Red Data species, but no longer applicable.

Bibliography. Anderson, M.D. (1994), Brooke (1968, 1969a, 1969c, 1970a, 1971b, 1971c, 1984), Brooke & Avery (1992), Brown (1989, 1993), Dean & Jensen (1974), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Fry *et al.* (1988), Ginn *et al.* (1989), Harrison *et al.* (1997), Lack (1956a), Louit (1980), Mackworth-Præd & Grant (1962), Maclean (1993), Pinto (1983), Ryan & Rose (1985), Snow (1978).

86. Pacific Swift

Apus pacificus

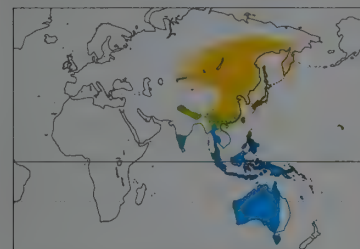
French: Martinet de Sibérie **German:** Pazifiksegler **Spanish:** Vencejo del Pacífico
Other common names: Fork-tailed Swift(!), Pacific Fork-tailed Swift, White-rumped Swift(!), Asian/Large/Northern White-rumped Swift

Taxonomy. *Hirundo pacifica* Latham, 1801, New South Wales.

Forms superspecies with *A. acuticauda*, with which in past occasionally considered conspecific. Four subspecies recognized.

Subspecies and Distribution.

A. p. pacificus (Latham, 1801) - Siberia E to Kamchatka and Japan, S to N China and S Japan; winters in Indonesia, Melanesia, Australia and possibly NE India (Assam, Nagaland, Manipur).
A. p. kanoi Yamashina, 1942 - SE Tibet E to Taiwan; winters in Malaysia, Philippines and Indonesia.
A. p. leuconyx (Blyth, 1845) - outer Himalayas and Assam hills; winters in India.
A. p. cooki (Harrington, 1913) - SE Asia; winters S to N peninsular Thailand.
May also breed (race unknown) in Batan Is (N Philippines).



Descriptive notes. 17-18 cm; male 42.5 g, female 44.5 g. Large swift, with rakish structure, long pointed wings, long, deeply forked tail, and thickest outer tail tapering little from body. Very black upperparts, tail and wings, showing greater contrast between inner wing and outer wing below, with striking white rump band; feathers of underparts broadly white-fringed, though whitish throat-patch can be indistinct. Race *kanoi* blacker, with rump-patch and throat-patch smaller, greyer throat and more streaked and less deeply forked tail; *leuconyx* similar to *kanoi* but smaller; *coki* smallest race, with most streaking on throat and

rump and narrowest underpart fringing.

Habitat. Occurs over a vast range of habitats, both breeding and wintering, from low Arctic to pebbles, often around human habitation. Winters mainly in lowlands. Recorded breeding at 2300 m in Pakistan and c. 3500 m in Tibet; recorded to 3800 m in Nepal and may forage as high as 4000 m; occurs over temperate, subtropical and broad-leaved forest between 1300-2400 m in C Bhutan; occurs from sea-level to 3000 m in Japan.

Food and Feeding. On Chinese breeding grounds, prey recorded from 9 insect orders, Diptera predominating. Flying termites recorded for race *leuconyx*, and bees in Myanmar in winter. In Siberia where sympatric with *A. apus*, feeds at dusk for much longer period, to midnight or 1:00 am. Typically forages higher than congeners, especially in winter. In Malaysia, mean foraging heights 184.5 m in forested habitats and 133.5 m in open habitats, most preferring former, representing higher strata in mixed flocks with *Hirundapus*, *A. nipalensis* and to lesser extent *Rhaphidura leucopygia*. Gregarious, regularly in large flocks, though most often found foraging in small groups of 3-5.

Breeding. Breeds Langtang in Nepal, Mar-May, Himalayas Apr-Jul, and Japan Jun-Aug; eggs recorded from late May on Yellow Sea islands, from early to middle Jun in China, from mid-Jun in L. Baikal region, and mid-Jun to mid-Jul in Siberia; nestlings being fed in mid-Jul near Ust-Karsk. Colonial. In Japan, nests in mountainous cliffs and caves on islands; nest is half-cup of vegetable matter agglutinated with saliva and similarly adhered to sloping face of cliff fissure or cave of building; will utilize nest of Nepal House-martin (*Delichon nipalensis*); nest material taken in flight and from ground. Clutch 1-3; incubation 17 days; both adults take equal part in all duties at nest; fledging period 40-5 days. On Cheniushan I in Yellow Sea, where conditions apparently highly suitable, hatching success 73.5%, fledging success 63.6%, with average of 1.24 young produced per pair annually.

Movements. Nominate race a long-distance migrant, while 3 more S races mainly resident or short-distance migrants; race *coki* thought to be resident, but has occurred in winter in Malay Peninsula; *kanoi* has occurred in winter in Philippines and Malaysia; *leuconyx* may be dispersive resident, recorded throughout Indian Subcontinent. Nominate form winters in Indonesia, Melanesia and Australia, where common Oct-Apr; recorded Cape York Peninsula, N Australia, with *Hirundapus caudacutus* in Jul, presumably non-breeding birds. Arrives in Japan from late Mar, most arriving in Honshu mid-Apr and Hokkaido early May. First arrivals in far E Siberia from late Apr to early May, appearing *en masse* in NE Mongolia late May to early Jun. Leaves Yakutia in mid-Aug, E Mongolia Aug, L. Baikal late Aug, Japan from late Sept with migration through Oct and early Nov. Regular passage migrant in Java, though relatively few migrant records from Borneo and Sumatra. Recorded across Wallacea, rarely as winter visitor but mainly as passage migrant: Sulawesi Sept-Oct and Jan-Mar, Halmahera late Sept and early Apr, Buru late Nov and early Dec, Flores mid-Aug to mid-Apr, Timor Sept-Nov and Mar, and Aru Is early Apr. Migrates through Malay Peninsula mid-Sept to mid-Nov and late Feb to late May, recorded Talaud early Oct and S New Guinea mid-Oct to late Dec. Large numbers migrate through Riau Archipelago, in Strait of Malacca, late Apr. Often seen with *Hirundapus* species on passage. First mainland record in Cochinchina as recently as 1996, and probably under-recorded on passage throughout Indochina. Recently recorded in mid-winter in S Sumatra, where largest migrant group c. 220 moving S through Serkap early Oct. Vagrant within Russia W to Urals, to Britain Jun 1981 and May 1993, to Alaskan islands at least 10 times, Jun-Sept, and to Macquarie I in S Tasman Sea.

Status and Conservation. Not globally threatened. Rare in Pakistan, but not uncommon in other Himalayan areas. Generally common throughout rest of breeding and wintering range. Large colony on one Yellow Sea island numbers over 8000 birds after breeding.

Bibliography. Abdullah (1963), Ali & Ripley (1983), Ali *et al.* (1996), Beehler *et al.* (1986), Bent (1940), Biswas (1974), Blackburn (1970), Blakers *et al.* (1984), Brazill (1991), Brooke & Steyn (1979), Chantler (1993), Cheng Tsohsin (1987), Cheng Zhaoqing & Zhou Benxiang (1987), Clapp (1989), Coates (1985), Coates & Bishop (1997), Craugh (1985), Davison (1997b), Deignan (1945, 1956), Dementiev & Gladkov (1951), Diamond & Bishop (1994), Dickinson *et al.* (1991), Driessens (1994), Duckworth *et al.* (1998), Dudley *et al.* (1996), Étchécopar & Hue (1978), Feare (1979), Flint *et al.* (1984), Gantlett (1993), Gao Wei *et al.* (1981), Gao Yuren & Zhou Benxiang (1985), Gibson (1981), Green, M. (1995), Grimmett *et al.* (1998), Higgins (1999), Holmes, D.A. (1994b, 1996, 1997), Inskipp & Inskipp (1991), King (1984), Knystautas (1993), Lack (1956a, 1958e), Lekagul & Round (1991), Litvinenko & Luleyeva (1992), Luleyeva (1993), van Marle & Voous (1988), Mayr & Rand (1937), Medway & Wells (1976), Mees (1973, 1982b), Nuytemans (1998), Parker (1990), Parrott & Andrew (1996), Primrose (1921), Robertson (1980), Roberts (1991), Robson (1995c, 1996c, 1997a), Rogacheva (1992), Shivraj Kumar (1964), Skerrett (1996), Smythies (1981, 1986), Snow & Perrins (1998), Stepanyan (1990), Strahan (1994), Tian Gengwu (1986), Tymstra *et al.* (1997), Vaurie (1965), Waugh & Hails (1983), Wells (1999), White & Bruce (1986), Yamashina (1982), Zakharov (1995), Zhao Zhengjie (1995).

87. Dark-rumped Swift

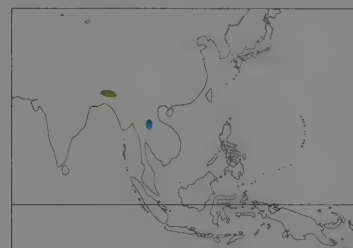
Apus acuticauda

French: Martinet de l'Assam **German:** Glanzrückensegler **Spanish:** Vencejo de los Khasi
Other common names: Khasi Hills/Dark-backed Swift

Taxonomy. *C. [ypselus] acuticauda* [sic], Jerdon, 1864, India (= Nepal?).

Forms superspecies with *A. pacificus*, of which in past occasionally considered a race. Population from Blue Mts, in Lushai Hills of S Assam, described as race *rupehandi*, but claimed differences in plumage do not hold good. It is also suggested that, if a series of specimens were available from Thailand, they might show that population to represent a separate form. Monotypic.

Distribution. Breeds with certainty around Cherrapunji and Lilancote, in Khasi Hills (NE India); also thought to breed in Lushai Hills, in Mizoram (extreme S Assam), where series of specimens collected in May. Recently recorded in Bhutan; may occur in Myanmar and (1 specimen) Nepal. In Thailand, to date only known by winter records from NW.



Descriptive notes. 17 cm. Large swift with rakish structure very like *A. pacificus*; outer tail slightly less thickset as outer rectrices strongly emarginated. Upperparts black; underparts heavily marked with broad white fringes; throat-patch indistinct, more heavily streaked and probably averaging darker than in *A. pacificus*.

Habitat. Deep gulleys and cliffs in the very wet Khasi Hills.

Food and Feeding. Not known.

Breeding. Season end Mar to end Apr. Colonial. Cup-like nest of grass and feathers agglutinated with saliva, on ledge in cliff fissure.

Clutch 2-3, though 4 recorded.

Movements. Winter records from NW Thailand indicate short-distance migration, although birds concerned may possibly represent an unknown population. Recorded from Bhutan in springs of 1996 and 1997; not recorded from Andaman Is, and some doubts surround origin of Nepalese record. May be summer visitor only to breeding zone.

Status and Conservation. VULNERABLE. Restricted-range species; present in Eastern Himalayas EBA. Apparently small population and very limited known range imply species at risk, though lack of recent information may mask true status. Extensive research and survey work required.

Bibliography. Ali & Ripley (1983), Baker (1934a), Brooke (1969d), Collar & Andrew (1988), Collar *et al.* (1994), Grimmett *et al.* (1998), Inskipp, C. & Inskipp (1991), Inskipp, T. *et al.* (1996), Jerdon (1863-1864, 1871), Koelz (1954), Lack (1956a, 1958e), Lekagul & Round (1991), Ripley (1982), Robson (1996b, 1997d), Smythies (1986), Stattersfield *et al.* (1998), Vaurie (1959).

88. Little Swift

Apus affinis

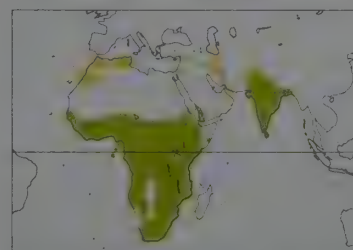
French: Martinet des maisons **German:** Stubbstärtssegler **Spanish:** Vencejo Moro
Other common names: House Swift(!)

Taxonomy. *Cypselus affinis* J. E. Gray, 1830, Ganges.

Forms superspecies with *A. nipalensis*, with which often considered conspecific; separation based mainly on consistently shorter, less forked tail and broader rump band, combined with potential sympatry in Himalayas. Birds of sub-Saharan Africa formerly treated as race *abessynicus* [sic], and those of coastal Limpopo and Transkei as race *gyratus*. Six subspecies recognized.

Subspecies and Distribution.

A. a. galilejensis (Antinori, 1855) - NW Africa E to Pakistan, and S of Sahara in E Sudan, Eritrea, Ethiopia and NW Somalia.
A. a. aerobates Brooke, 1969 - Mauritania E to Somalia and S to Transkei (E South Africa).
A. a. bannermani Hartert, 1928 - Bioko, Principe and São Tomé, in Gulf of Guinea.
A. a. theresae Meinertzhagen, 1949 - W & S Angola to S Zambia and S through S Africa.
A. a. affinis (J. E. Gray, 1830) - S Somalia to N Mozambique (including Zanzibar and Pemba), and E to India S of Himalayas and E of Pakistan; some birds winter in India and presumably Africa.
A. a. singalensis Madarász, 1911 - S India and Sri Lanka.



Descriptive notes. 12 cm; male 25 g, female 25 g. Small swift with relatively chunky body, blunt wing-tips and square tail; black above, with slightly paler forehead and uppertail-coverts, and very distinct broad white rump-patch, which extends onto lower part of flanks; underparts blackish apart from inner wing and rounded white throat-patch. Differs from other *Apus* in square-ended tail; rump-patch broader than in *A. nipalensis*. Race *galilejensis* very pale, especially on tail-coverts and forehead; *aerobates* darker than nominate, especially on wings and tail, with coastal population between Limpopo and Transkei ("*gyratus*") darkest and

largest within subspecies; *theresae* very like *galilejensis* but with slightly darker uppertail-coverts; *bannermani* darkest race, with heaviest throat streaking; *singalensis* blacker than nominate, especially on head and uppertail-coverts, some showing slight tail-fork.

Habitat. Occurs over a wide range of habitats and latitudes, though less frequently in truly arid regions, and usually close to human habitation. In Kenya, recorded to 3000 m. In Botswana, absent from areas lacking surface water as a result of permeable sandy soils. May shun high-altitude grassland in South Africa because of competition from wintering Northern House-martins (*Delichon urbica*).

Food and Feeding. Flies, termites, ants, beetles, grasshoppers and a dragonfly recorded in Africa, and Diptera, Hemiptera, Coleoptera, Hymenoptera and airborne Arachnida in India. Rarely feeds very low but often forages at great height, particularly, it is believed, during winter in S Africa. Highly gregarious, often with other Apodidae. Noted feeding in flocks of up to 50 on huge columns of "Chilli" white aphids (*Myzus persicae*) in S India. Forages as far as 15-20 km from nest-site on occasions.

Breeding. Feb-May and Aug-Oct in Mauritania, Oct-Jul in Senegambia, avoiding rainy season, and year-round in W African rainforest areas, including Liberia, where Aug-Sept lull; laying dates Mar-May and Sept-Oct in Sierra Leone, May and Dec in Nigeria (perhaps year-round, at least in S),

Feb in Bioko, Jun-Jul in São Tomé, Jun in Chad, Mar and May in Sudan, and Mar-May and Jul-Aug in Ethiopia; E African breeding coincides with rainy seasons, Feb in Malawi, Oct and Mar-Apr in Zambia, Sept-May in Zimbabwe; Aug-Apr in South Africa, with two-thirds Sept-Nov; nominate race breeds year-round in India except Nov-Feb; *singalensis* breeds mainly Mar-Jul; *galilejensis* from Feb/Mar to Oct in Karachi, Mar-Jul in NW Africa, and from early May in Nura-Tau range (Uzbekistan); in Israel, first brood hatches late Mar to early Apr and second Jun-Jul; nestlings being fed mid-Aug, Turkmenistan. Two breeding seasons recorded in Kenya and Gujarat as result of bimodal rainy season. Colonial, typically fewer than 30 nests, though colony of 95 recorded and c. 1000 nests from 1 building in Ghana; nesting alongside Eurasian Crag-martin (*Hirundo rupestris*) reported; 2-3 females may lay in 1 nest; solitary breeding recorded. Cliff sites and abandoned swallow (*Hirundo*) nests can be employed and forcible eviction noted, but typically nests on man-made structure in angle between roof and wall; eviction by House Sparrows (*Passer domesticus*) recorded. Nest a sturdy, untidy, yet internally neat and smooth, hemispherical "bag" of vegetable matter, mainly grass, down and small twigs, with feathers, agglutinated with saliva; built in dense, often overlapping clusters with up to 3 entrances, sometimes communal; needs perch to cling to while building. Clutch 1-3, 3 in Kenya and 2 in South Africa, usually completed over 4-5 days, all eggs in colony laid within 10 days; incubation stints short and irregular until clutch completed, and then initially for up to 90% of day, by both parents typically at intervals of less than 90 minutes; clutch unattended c. 3 times per day, sometimes for up to 1 hour (usually less than 8 minutes); incubation 22-24 days. Double-brooded, second clutch laid on fledging of first young; in Zanzibar 1 pair laid 6 clutches over 21 months, implying near-constant breeding in some equatorial areas.

Movements. Resident throughout tropics; majority of northernmost (W Palearctic) and southernmost (S African) populations wholly or partly migratory. Present Turkey Mar-Sept only, and summer only also in Tajikistan, Uzbekistan and Turkmenistan, otherwise partially migratory only in Middle East and N Africa, though noted on passage in Chad during Oct. E populations of *galilejensis* may migrate through Arabia to Africa. Complex picture emerges from Israel, where resident N Israeli population disperses up to 100 km during Oct-Mar into areas where it does not breed; small passage, presumably from outside Israel, mid-Sept to mid-Dec and early Feb to mid-May. Populations in S Africa, C Zimbabwean plateau and Freetown, Liberia, may be partly migratory, but this is equivocal and may be result of apparent reductions in numbers caused by changes in roosting behaviour, making species less conspicuous; however, coastal migration recorded in Liberia at beginning of dry season. Recently recorded Antananarivo, Madagascar, during Sept and Nov; at least one record on Maldives, flock of 7 in Dec. Accidental but increasingly recorded in Europe; 5 records in Spain up to early 1990's and at least as many since; 4 in Portugal up to Jun 1998, with first as recently as 1995; Italy 2, Malta 8, Britain and Ireland 9 (May-Nov) and Sweden 4 (Jun-Nov) up to early 1990's, and recent increase in British records (5 in 1997 and 3 in 1998).

Status and Conservation. Not globally threatened. Scarce to locally common in W Palearctic, though often abundant in towns and cities in tropical range. Although generally common and locally abundant in sub-Saharan Africa and India, more local in rural areas. Huge population increase in Africa during 20th century due to increasing use of buildings; in South Africa recorded only once in 19th century, though expanded rapidly to become common by 1930's, with continued expansion to present day; very similar story from Liberia, where expansion followed mass forest destruction. Israeli population believed to number in low thousands of pairs. In Saudi Arabia commonest in Asir highlands. Evidence of genuine increase in W European records in recent years, and possible breeding in S Spain in 1995, when 2 seen flying around a rocky area in Sierra de la Plata, near Tarifa, occasionally entering holes; other recent records from this area, which also holds small breeding population of *A. caffer*.

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89. House Swift

Apus nipalensis

French: Martinet malais **German:** Haussegler **Spanish:** Vencejo Oriental
Other common names: Little Swift(!), Malay House Swift

Taxonomy. *Cypselus Nipalensis* Hodgson, 1837, central region of Nepal.

Forms superspecies with *A. affinis*, with which often considered conspecific; separation based mainly on consistently longer, more forked tail and narrower rump band, combined with potential sympatry in Himalayas. Four subspecies recognized.

Subspecies and Distribution.

A. n. nipalensis (Hodgson, 1837) - Nepal E to SE China (Fujian) and Japan, S through Assam and SE Asia, and also N Philippines.

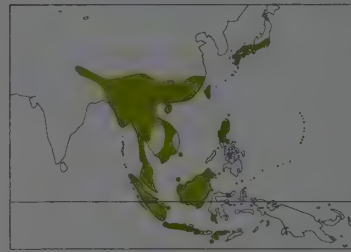
A. n. subfuscatus (Blyth, 1849) - Malay Peninsula, Sumatra including Riau Archipelago and Belitung, Anambas, N Natunas and Borneo.

A. n. fuscatus Brooke, 1971 - Java and Bali.

A. n. kuntzi Deignan, 1958 - Taiwan.

Also occurs in Sulawesi and Lesser Sundas, where population may refer to *subfuscatus* or *fuscatus*.

Descriptive notes. 15 cm. Very similar in size and structure to *A. affinis*, but tail averages longer and has slight, though usually discernible, fork; blacker than *A. affinis*, notably on head and tail-coverts, with narrower white rump band. Race *subfuscatus* even blacker than nominate, especially on upper head; *fuscatus* has deepest tail-fork and browner underparts; *kuntzi* intermediate between nominate and *subfuscatus*, with most heavily streaked rump of any subspecies.



sometimes with other Apodidae and hirundines. In Malaysia in Feb-Jul forages in high strata (over 30 m), with mean heights of 185 m over forested areas and 114.5 m over open areas; preference for forest during Feb-Mar, reversed in Apr.

Breeding. In Myanmar, breeds any time between Feb and early Oct, with most nest-site selection in late Mar, nest-building in Apr, laying in May, hatching in Jun and most nestlings fledged by Jul; in Japan, breeds Apr to late Nov, with hatching peaks late May to early Jun, late Jul to early Aug and late Sept to early Oct; possible prospecting in late Jun, Batangas (Philippines); occupied nests from mid-Dec to mid-Aug, Malay Peninsula; eggs Mar-Apr in Sumatra; nest completed by early Feb with fledging in late Jun, Borneo. Colonial, with breeding synchronized within colony. Typically nests in angle between roof and wall in man-made structure, often in seemingly dangerously accessible sites where human population tolerant; in Yunnan at elevation of 3.6-15.5 m, average 8.1 m; old nest of Striated Swallow (*Hirundo striolata*) used on Flores. Large untidy hemispherical nest "bags" in overlapping clusters, constructed of vegetable matter and feathers, sometimes with artefacts such as rags incorporated, agglutinated and adhered with saliva. Clutch 1-5, mean 3.1; incubation 18-26 days, average 21.1; mean of 26 feeding visits per day, range 8-55; fledging period 36-51 days, average 43.6. Typically raises more than 1 brood per year, with 3 broods in Japan. Hatching success 89.5%.

Movements. Some N populations undertake poorly studied winter movements, with records during this season in Indian Subcontinent. Believed to be a winter resident in Luzon. Recorded in N Australia.

Status and Conservation. Not globally threatened. Abundant over most of range, though level of abundance appears to vary considerably. Common on Sumatra but rather locally distributed. Rare and local in Philippines. Uncommon and highly localized in Japan, where first recorded in 1965, but range expanding since 1970's and 1980's following arrival of Red-rumped Swallows (*Hirundo daurica*), in whose old nests it breeds. Recent colonist in Brunei, where 3 colonies by 1977, but expansion very slow as only 1 additional colony found since then. Recent colonist also in Wallacea, first recorded with certainty in 1978 on Sulawesi, where scarce and local resident in N & S. Similar story from Lesser Sundas, where recorded on Flores since 1986 and on Timor in 1993, and colony of 50 birds on Sumba in Jun 1994.

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90. Horus Swift

Apus horus

French: Martinet horus **German:** Horussegler **Spanish:** Vencejo Horus
Other common names: Toulson's Swift ("toulsoni"); Loanda Swift (*fuscobrunneus*)

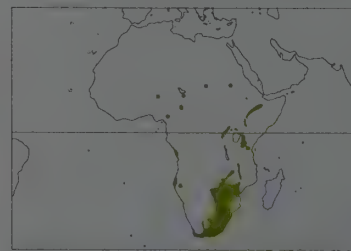
Taxonomy. *Cypselus affinis* var. *Cypselus Horus* Heuglin, 1869, north-east Africa.

Taxonomic status of form "toulsoni" of NW Angola and Zimbabwe is highly controversial, and it has been considered a full species, but is probably best treated as a dark morph within nominate race. Two subspecies currently recognized.

Subspecies and Distribution.

A. h. horus (Heuglin, 1869) - C Ethiopia, CS Kenya and N Tanzania, and NW Uganda to Burundi and E Zaire; Zambia to SW Cape (South Africa); more isolated populations in Nigeria, N Cameroon, W Chad, W & EC Sudan, extreme W Zaire and NW Angola.

A. h. fuscobrunneus Brooke, 1971 - SW Angola.



Descriptive notes. 15 cm; 26 g. Small, fork-tailed swift, black-brown with broad white rump-patch, white throat-patch. Differs from *A. affinis* in larger size, forked tail and relatively paler underwing-coverts; tail broader, relatively shorter and less deeply forked than in *A. caffer*. Race *fuscobrunneus* has dark brown rump, smaller, greyer throat-patch, lacks distinct gloss to plumage and has relatively paler uppertail-coverts and head; "toulsoni" morph similar to this subspecies but generally darker; intermediates between "toulsoni" and typical nominate birds have been seen in Zimbabwe.

Habitat. Correlates with that of the bee-eaters (Meropidae), kingfishers (Alcedinidae) and martins (Hirundinidae), among which it nests; consequently, often seen around sand banks, feeding over wide range of adjacent habitat. In Kenya, utilizes colonies of White-fronted Bee-eaters (*Merops bullockoides*) and has a similar range. Breeds at 1600-2000 m in C Kenya.

Food and Feeding. Termites, flies, beetles and ants recorded. One food ball contained 204 insects: 78 jassid, 1 fulgorid and 5 heteropteran bugs, 5 Neuroptera, 95 Lepidoptera, 3 Diptera, 1 wasp, 1 beetle and 15 indeterminate. Another contained 12 spiders and 477 insects of 15 families: beetles, butterflies, flies and wasps, of which 77% Cicadellidae. In Kenya, a complete bolus of 363 prey items and a partial bolus of 33 comprised 79% termites (Termitidae), planthoppers (Cicadellidae and Delphacidae) and ants (Formicidae). Foraging level in mixed flocks typically between lower *Cypsiurus parvus* and higher *A. caffer*; this was apparent at Kariba, Zimbabwe, where fed in groups

of 4-10 within same stratum, 20-30 m, as Mosque Swallow (*Hirundo senegalensis*). Occasionally feeds at highest level, 30-40 m, when this not already occupied. Forages in small flocks, up to 30, often with other swifts or hirundines.

Breeding. Breeds Chad Nov-Feb, Sudan Mar-Jun; egg-laying Jun in Ethiopia, Apr-May in Malawi, Aug-Sept in Zambia, all year but mostly Nov-Feb in Zimbabwe, Jan-May in Transvaal, Nov-Dec and Mar-Apr in Cape; in Zimbabwe breeds in hot wet months Oct-Apr above 1000 m, and in cool months Apr-Sept below 1000 m. Nests solitary; although not genuinely colonial, also in small groups typically of up to 12 pairs, sometimes many more, often scattered within colonies of bee-eaters (Meropidae) or sand martins (*Riparia*), grouped nesting therefore believed to result from utilizing nest-holes of colonial species. Apparent breeding behaviour noted from a cave in coastal sandstone cliffs, SW Cape. Uses deserted nests of burrowing species, namely bee-eaters, kingfishers (Alcedinidae), Ground Woodpecker (*Geocolaptes olivaceus*), Banded Martin (*Riparia cincta*) and probably Southern Anteater-chat (*Myrmecocichla formicivora*), typically in riverbanks; eviction not recorded, though may lose nest to African Pied Starlings (*Spreo bicolor*); 1 burrow was 45 cm long, with narrow entrance and terminal disc-shaped nesting cavern, 30 x 40 cm and 6 cm high. Nest is thin platform of vegetable matter agglutinated with saliva to hair, feathers, occasionally rags; windblown grass collected. Copulates at nest. Clutch 1-4, average 2 in Zimbabwe and 3 in South Africa; incubation c. 28 days; average feeding interval 54 minutes, mean weight of food pellets 1 g; fledging period c. 6 weeks.

Movements. Populations breeding in South African and Zimbabwean high veld winter elsewhere, possibly in Zimbabwean low veld, though resident in some low-lying tropical parts of S Africa S to NE Transvaal. Similar movements, thought to be localized, perhaps altitudinal, occur in parts of E Africa, e.g. present at Mau Narok, Kenya, at 3000 m late Apr to early Jul; C Kenyan population as a whole present only Mar-Sep, with some records E of breeding range Oct-Dec. Believed to be dry-season visitor in Zambezi Valley. In Natal, makes altitudinal migration from 1500-2400 m to below 900 m. **Status and Conservation.** Not globally threatened. Locally common in suitable habitat over much of range, and abundant in some C Ethiopian highland sites. Range has increased following colonization of buildings by hirundine hosts. One Kenyan colony at Nakuru numbered "several hundred" pairs in 1978. Recently recorded for first time from Niger.

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91. White-rumped Swift

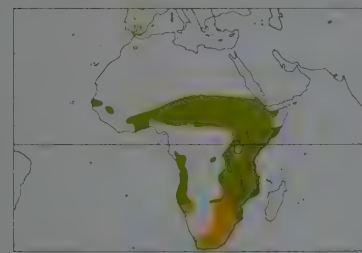
Apus caffer

French: Martinet café **German:** Kaffernsegler **Spanish:** Vencejo Café
Other common names: African White-rumped Swift

Taxonomy. *Cypselus Caffer* Lichtenstein, 1823, South Africa.

Population of N Angola and lower Congo formerly separated racially as *ansorgei*, but merely one of darkest-headed populations and no longer considered a valid race. Birds of tropical zones (excluding migratory populations in extreme N and S) claimed to average shorter-winged, and are sometimes recognized as racially distinct (*streubelii*), but variation in wing length apparently clinal, increasing from N to SW. Monotypic.

Distribution. S Spain, E Portugal and C Morocco; Senegambia, N & E Sierra Leone and (probably breeding) NW Liberia, then C Ivory Coast E to Somalia and S to South Africa; S Gabon S to C Namibia (Windhoek). Winter range of migratory populations unknown.



Descriptive notes. 14 cm; 22 g. Smallish, very graceful swift with long, deeply forked tail, very heavily emarginated outer rectrices, often held tightly closed for long periods, and long slim wings. Deeply black plumage with narrow, though highly contrasting, white rump, small white throat-patch, and slightly paler forehead and superciliary area; when remiges fresh, white trailing edge to secondaries visible.

Habitat. Occurs over a wide range of habitats, from arid savanna and Mediterranean scrub to equatorial forest. Habitat dictated by preferences of nest "hosts": *A. affinis*, and Lesser Striped Swallow (*Hirundo abyssinica*), Greater

Striped Swallow (*H. cucullata*), Rufous-chested Swallow (*H. semirufa*), Wire-tailed Swallow (*H. smithi*), Rock Martin (*H. fuligula*), Angolan Cliff Swallow (*H. rufigula*) and Red-rumped Swallow (*H. daurica*). Often around urban areas in sub-Saharan Africa, but not yet in W Palearctic (though will nest in disused buildings). In Morocco, occurs from sea-level to 2500 m.

Food and Feeding. Three food balls contained a cerropid bug and 33 winged ants averaging 8 mm in length, a number of winged fire ants (*Solenopsis puncticeps*), some still alive, 10 spiders, and 98 other insects comprising 17 families of flies, bugs, beetles and wasps, of which c. 75% by weight were the leafhopper *Glossocratus afzeli*. Other recorded prey items include termites, chalcid wasps (Chalcidoidea), bees, Lepidoptera and weevils (Curculionidae). Commonly associates with other Apodidae, and less often within W Palearctic range with *H. daurica*. Occurs within the highest feeding level at Kariba (Zimbabwe), 30-40 m.

Breeding. In Spain breeds from late May; laying dates May in Morocco, Jul in Senegambia, Apr and Jun-Jul in Nigeria, Feb in Sudan, May-Jun in Ethiopia, May and Jul in Zaire, Jan-Feb, Aug and Oct in Angola, Aug-Dec in Zambia, Sept in Malawi, Aug-Apr in Zimbabwe, Nov-Feb in Namibia, Aug-Mar in Transvaal, with South African peak Oct-Jan. Loosely colonial or solitary, maximum colony size 15-20; minimum distance between nests 2.5 m in South Africa and 25 m in Spain; loyal to nest-site for at least 9 years and to mate for at least 3. Typically uses disused *A. affinis* or certain swallow (*Hirundo*) nests, though niches in rock-faces or buildings sometimes used; eviction of

swallows involves repeated attacks lasting 3-5 minutes, several times during day, with 4-6 swifts clinging to entrance while owner in occupation; other strategy is to occupy recently completed nest when builder leaves and then remain inside, lining entrance with feathers to hinder entry. In disused nests, uses feathers and down adhered with saliva as lining; in rock sites, shallow cup of feathers and vegetable matter agglutinated with saliva; under eaves, nests only against masonry; typically uses retort-shaped nests, though more open ones may be adopted with suitable adjustment involving building of side walls. Clutch 1-3 eggs, usually 2, laying interval 38-72 hours; sexes share nest duties equally; time spent incubating highly variable, typically 17-90%; average incubation period 21 days in Tanzania and 22-5 days in South Africa, second egg hatching up to 30 hours after first; chicks soon after hatching very active, later moving within cavity up to 2-3 m from nest; eyes open from 7-8 days, fully open but milky by day 14, feathers open on head day 11, belly and tail day 12, chin and remiges days 14-15, and back day 22, when some grey down still visible; down no longer present by day 31; brooding fairly continuous in first week, becoming irregular by third; average fledging period 42 days in Tanzania and Zimbabwe, 46 days in South Africa, with great variation in interval between 2 fledglings leaving nest (4 hours to 22 days). Double-brooded in parts of range; in Tanzania 3 broods noted, re-laying interval 2-7 days; 2 or perhaps 3 broods in Spain. Success rate 76% in Tanzania and 57% in South Africa; mean annual production 2.5 young, with average 1-1.5 young fledged per breeding effort. Breeding can commence from 2 years of age.

Movements. Migratory in northernmost and southernmost parts of range. Spanish population present early May to Aug-Oct, some recorded into early Dec, with autumn migration through Straits of Gibraltar mid-Aug to mid-Oct; S African population present Aug-May, mainly absent from S Cape and much reduced farther N within S breeding range Jun-Jul. Poorly understood wet-season movements into Sahel may be feature of N sub-Saharan populations. Otherwise resident. Migrates in flocks of up to 100. S African migrants may be transequatorial. Some degree of altitudinal migration in Natal. First record from Arabia 1982, and seen at least once subsequently in Tihamah coastal plains, Saudi Arabia, in Mar 1989. Vagrant to Norway (May, Jun) and Finland (Nov).

Status and Conservation. Not globally threatened. In sub-Saharan Africa localized in wide W African range, increasing in E Africa where commonest swift away from urban areas, and common in S Africa, where population increase primarily result of utilization of bridge construction. Highly localized and scarce in W Palearctic, though increasing in both range and density. Strait of Gibraltar area believed to hold at least 30 breeding pairs, with highest density of 10 pairs in zone with radius of 3 km; Spanish population estimated at 30-100 pairs in early 1990's; breeding confirmed in Portugal in 1995.

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92. Bates's Swift

Apus batesi

French: Martinet de Bates **German:** Mohrensegler **Spanish:** Vencejo del Camerún
Other common names: Black(!) Bates's Black Swift

Taxonomy. *Cypselus batesi* Sharpe, 1904, Efulen, Cameroon. Monotypic.

Distribution. W Cameroon and N Gabon, Central African Republic, and E Zaire (Kivu Province and Semliki Valley); also Sierra Leone to Nigeria, where status uncertain.



Descriptive notes. 14 cm. Small swift with structure most similar to *A. caffer*, with deeply forked tail; distinctive high-speed flight with rapid flickering wingbeats and occasional short glides. Very black plumage relieved only by typical underwing contrast and indistinctly paler throat-patch. Plumage the most uniform of any *Apus*.

Habitat. Occurs in rainforest zone near rocky extrusions where cliff swallows, especially Dusky Cliff-swallow (*Hirundo fuliginosa*), present. In N Liberia, reported at 500-1500 m.

Food and Feeding. Not known.

Breeding. Breeds Sept-Mar in Gabon, probably Mar and maybe Jan in Liberia, and lays May-Jun in Cameroon. Solitary, nesting in deserted nests of *H. fuliginosa* and probably Lesser Striped Swallows (*H. abyssinica*), which has led to suggestion that other hirundine nests may be used; recorded examining nests of *Telecanthura ussheri*. Lines nest interior and spout with feathers, seed-down and saliva. 2 white eggs.

Movements. Resident.

Status and Conservation. Not globally threatened. Generally rare, but abundance varies and can be locally frequent, with 20-30 birds seen along R Semliki (E Zaire) on three occasions in Oct during late 1930's. Commonest in highlands of Cameroon. Widespread but uncommon in N Liberia.

Bibliography. Bannerman (1931, 1953), Bates (1930), Brooke (1971b, 1971i), Brosset & Éraud (1986), Carroll (1988), Chapin (1939), Christy & Clarke (1994), Colston & Curry-Lindahl (1986), Dowsett (1989a), Dowsett & Dowsett-Lemaire (1993, 1997), Dowsett & Forbes-Watson (1993), Dowsett *et al.* (1999), Dyer *et al.* (1986), Elgood *et al.* (1994), Field (1998), Fry *et al.* (1988), Gatter (1988, 1997), Grimes (1987), Lippens & Wille (1976), Louette (1981), Mackworth-Præd & Grant (1970), Rodewald *et al.* (1994), Rougeot (1951), Serle (1954), Sharpe (1904), Smith & McNiven (1993), Snow (1978), Stuart (1986), Thollay (1985).

Class AVES

Order APODIFORMES

Suborder APODI

Family HEMIPROCNIDAE (TREESWIFTS)



- Small to large branch-perching swifts, partly glossy, with long wingtips that fold scissor-like across deeply forked tail; two species with erectile forehead-crest, others with facial plumes.
- 15-31 cm.



- Oriental Region E to Solomon Is.
- Deciduous savanna woodland to evergreen rainforest.
- 1 genus, 4 species, 13 taxa.
- No species threatened; none extinct since 1600.

Systematics

Obviously glossy above, with rather soft, songbird-like plumage and a branch-perching foot, the "halfway-house" treeswifts helped sustain a long period of confusion over swifts (Apodidae) and swallows (Hirundinidae), groups that taxonomists from Linnaeus to Temminck actually merged and whose relatedness remained controversial until the end of the nineteenth century.

The four currently recognized species of treeswift were all described for science between 1802, when the Grey-rumped Treeswift (*Hemiprocne longipennis*) was named by G. S. Rafinesque, and 1833, when S. R. Tickell separated the Crested Treeswift (*Hemiprocne coronata*). Remarkably, both of these, the first and last to be named, were placed in the old, inclusive genus *Hirundo*, making the Crested Treeswift possibly the last of many species ever to be wrongly classified as a swallow. Whatever his knowledge of the literature of the time, Tickell, then serving in India, would certainly have been the first describer of any treeswift species to have known a member of this family in the field, and so he may be said to have been misled for the very best of reasons.

C. L. Nitzsch's 1829 name of *Hemiprocne* (*hemi progne*, or "half-swallow") pre-dates most evidence for the phylogenetic remoteness of all swifts from swallows, but it validly refers to a treeswift and has priority over two rival family-group names used for these birds. Later, it came to denote more than just the treeswifts as now defined, and not until the 1890's were sound technical reasons put in place for assigning these peculiar birds to a taxonomic position of their own. In 1990, C. G. Sibley and J. E. Ahlquist summarized the history of this research, which had culminated in the recognition of two separate families of swifts. In terms of their anatomy, these two families in fact exhibit more differences from one another than are found among typical families of passerines.

Recognizable as a distinct group at a glance, the four treeswifts include one convincing superspecies that links the Grey-rumped and Crested Treeswifts. These two grey-and-glossy birds have nearly identical vocalizations, and a flap-like forehead-crest 2.5-3 cm tall that both sexes often raise when perched, no doubt as a behavioural signal to mates or others in the home tree. They show a small size difference overall, and differ also in details of face pattern, extent of glossy blackness on the upperparts, one or two minor colour-density features elsewhere, and the proportionate length of the tail-streamers. They were lumped for a time as allopatric representatives of a single species, but their ranges in south-west Thailand are now known to be contiguous, or may ac-

tually overlap, with no evidence of interbreeding. This apparent reproductive isolation is perhaps assisted by the predilection of the two species for mainly different habitats, the Grey-rumped preferring evergreen forest while the Crested selects deciduous growth. This situation is likely to continue west across the dividing range into south Tenasserim, but it has never been investigated there owing to problems over safety of access in that region.

The Whiskered Treeswift (*Hemiprocne comata*) and the Moustached Treeswift (*Hemiprocne mystacea*) are only slightly crested, but they share a bold face pattern. This is characterized by a white supercilium from the base of the bill to the nape, and a malar stripe from the chin along the jaw to the side of the neck, both formed of long hackle-points that trail clear of the head. Otherwise, since the Whiskered is the smallest member of the genus and the Moustached is the largest, these two are less similar to each other than are the two crested species. Moreover, the striped face pattern is actually incipient, though without hackle development, in the female Crested Treeswift, the male of which, however, lacks the malar stripe and shows white only above the lores.

Between them, the three larger species parcel out the family range almost in full. The Crested and the Grey-rumped Treeswifts are distributed parapatrically, their ranges meeting edge to edge in southern mainland South-east Asia, while the Grey-rumped and the Moustached Treeswifts are separated by a short water-gap in the western Moluccas. Only the Whiskered Treeswift occupies a mostly shared range, in which it is substantially smaller than the co-occurring Grey-rumped Treeswift. It differs from all of the larger species in its habitat preference, and operates a unique foraging technique that is presumably related to its small size. It is of interest that in the Philippines, where it is out of contact with the Grey-rumped Treeswift, the Whiskered averages larger in size than in its shared range, raising the suggestion that it may have taken up some vacant niche that would otherwise have been occupied by the Grey-rumped. Rather disappointingly, however, a brief description of the Whiskered Treeswift's foraging behaviour on the Philippine island of Negros gives no hint of the sort of behavioural shift that this species might have been expected to show had this expansion actually occurred.

Morphological Aspects

Technically, the four species of treeswift are distinguished from their relatives, the typical apodid swifts, by details of cranium

Unlike typical swifts, treeswifts are able to perch firmly on twigs and branches with the aid of a non-reversible hind toe.

They sit in rather an upright posture, and normally select a spot which gives them good all-round vision of their immediate surroundings. The Whiskered Treeswift, the smallest of the four species, is also the most active and manoeuvrable in flight, chasing insects and other small flying arthropods in amongst the twigs and leaves, usually staying close to the foliage, and well below the height of the main forest canopy.

[*Hemiprocne comata*
comata,
Johor, Malaysia.
Photo: Morten Strange/
NHPA]



shape; the form of the skeletal palate; the anatomy of the tarsus and deep plantar tendons operating the digits; the non-reversible hind toe associated with branch-perching; the lack of a claw on the manus; and the soft, passerine-like feathering, with a patch of downy plumage on the flank. As in typical swifts, the corner of the mouth runs well behind eye-level, to give a broad gape characteristic of an aerial insectivore. The feet and the shallow bill are black to dark purplish-slate, and the eyes are deep brown and proportionately large. The size of the eyes could be a reflection of the fact that foraging activity commonly reaches a peak in the late evening. All post-juvenile plumages are glossy blue- or green-shot black on, at least, the top of the head, the tail, the upperwing-coverts and the flight-feathers, with the tertials, their immediate coverts and the adjacent scapulars mainly whitish, forming a contrasting dorsal patch. Most species also show some white on the central belly or undertail-coverts, darker races of the Moustached Treeswift being the only exception in this respect.

Total length varies from 15-17 cm to 28-31 cm, and wing length from 12-14.5 cm in the Whiskered Treeswift to 19.5-24.5 cm in the Moustached Treeswift. Confining the comparison strictly to swifts, wing length is a reasonable index of wing area, and this combined with body weight can be used to calculate relative wing-loading, which is the amount of lift to be generated per unit wing area. In this case, the Moustached Treeswift, the only one for which reliable body weights have been published, has a lower wing-loading than a large typical swift of the genus *Apus*, and a very much lower one than a similar-sized needletail such as a *Hirundapus* species. This should hold true also for the middle-sized Crested and Grey-rumped Treeswifts, and it does fit with the amount of rather slow gliding and wheeling indulged in by those species while foraging and socializing on the wing. The rather vigorous, bat-like flapping of the little Whiskered Treeswift, on the other hand, is more like that of some small typical swifts in the same environment. On theoretical grounds, this species would not be expected to share the wing-loading advantage of its larger cousins, but this is speculation and the Whiskered Treeswift remains one of the most manoeuvrable fliers of all swifts.

As with typical swifts, most of the length of the treeswift wing is supplied by the primaries, the birds having a long manus but a relatively short arm. The Whiskered, Crested and Grey-rumped Treeswifts moult the primaries in standard swift fashion,

sequentially and descendantly, from the first primary at the carpal joint outwards to the leading edge of the wing. The large Moustached Treeswift, by contrast, regularly moults its primaries from two centres, covering the inner and the outer parts of the tract separately, and sometimes these centres are active together. Apart, perhaps, from reducing the total time taken to replace these feathers, this adaptation may aid in maintaining wing area, since it is unusual at any time to find a bird without a good proportion of its flight-feathers more or less fresh.

All treeswifts also show a remarkably deep forking of the tail. Depending on species, this accounts for 45% to 70% of the standard tail length, far in excess of the figure for any typical swift. Correspondingly long outer streamers, which, as in typical swifts, are narrower and more pointed in adults than in juveniles, give a tail length ranging from about 58% of wing length to, in the Moustached Treeswift, 85% of wing length. With individual variation, and sometimes even a length difference of a centimetre or more bilaterally, this swallow-like feature adds to these birds' manoeuvrability while foraging, an ability taken to extremes by the Whiskered Treeswift, as it works its way around details of the forest canopy "skin". At rest, the tail-points are often tightly adpressed, jutting out spike-like from beneath deeply crossed wingtips to give treeswifts their instantly recognizable shape on a perch.

In all species, the cryptic head and body plumage which characterizes juveniles is lost in a moult that begins soon after fledging, whereas the wing-coverts, flight-feathers and tail are retained until the complete moult of the following year. The juveniles soon lose their pale fringing through wear, and young birds are then aged most easily by the relatively broad, blunt-tipped shape of their tail-streamers (the fifth feather-pair, as in typical swifts).

Habitat

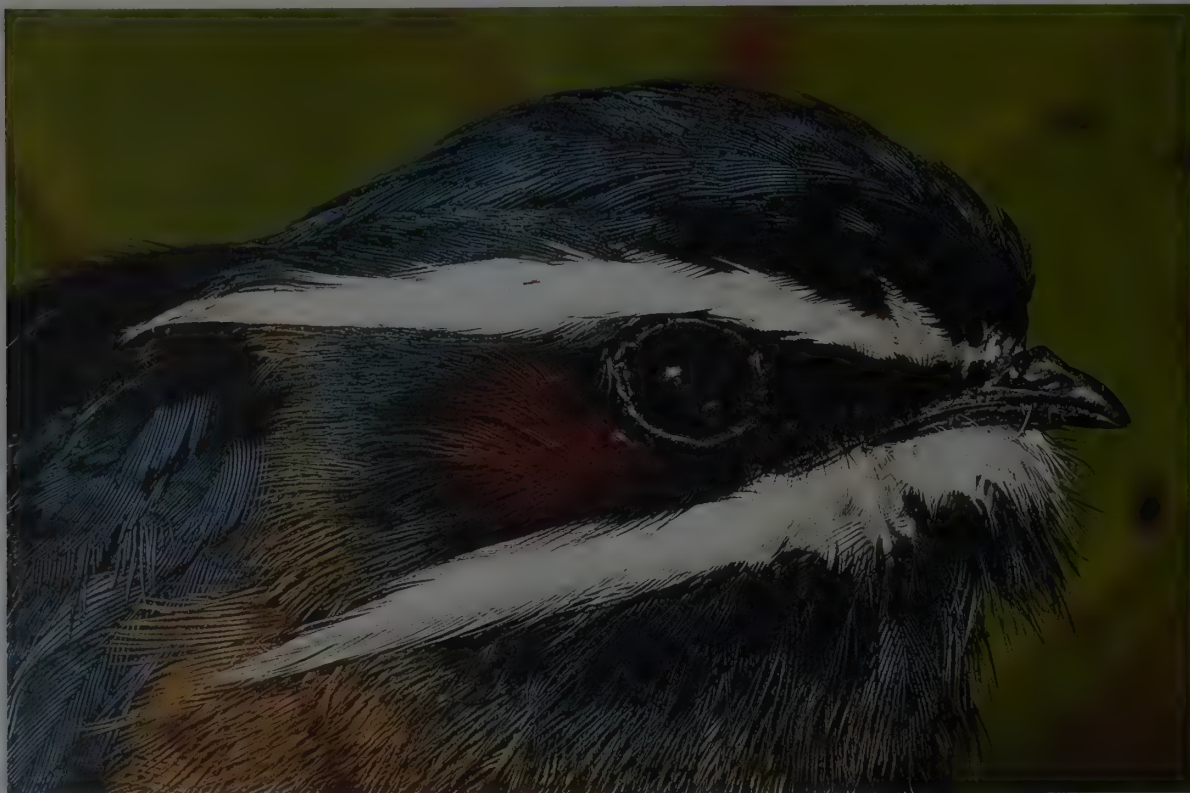
Although regularly occurring along logging tracks, streams and similar places sufficiently broad and open to break the canopy, the Whiskered Treeswift is a genuine member of the continuous-forest community, following vegetation surfaces up around the highest emergent crowns. Only very occasionally does it venture out into tall secondary growth or mature orchards, and even then typically into trees derived from local forest, such as durian. Nevertheless, in various parts of their ranges both the Whiskered and the Moustached Treeswifts have discovered service wires as a substitute for tree perches, but only where these pass through their normal habitat. Nowhere does this new behaviour appear to have expanded the foraging space that these birds exploit.

Among the larger species, the Crested Treeswift is the only one to make extensive use of deciduous forest types, dominated in India, for example, by the tree genera *Anogeissus*, *Boswellia* and *Tectona*. It is not, however, entirely confined to such habitat.



The flight silhouette of the Moustached Treeswift shows the narrow, curved wings and long tail streamers characteristic of the family. This relatively common species is found in parkland and partly cleared forest, and also in more "natural" habitats such as forest margins, mangroves and riverside woodland. It often hunts above the tree tops or over open country, and its typical flight behaviour involves much gliding.

[*Hemiprocne mystacea*
mystacea,
Veimaure River,
south-east New Guinea.
Photo: Brian J. Coates]



This Whiskered Treeswift illustrates several of the typical features of the genus *Hemiprocne*. The bill is very short, but the mouth extends well back to just below the eye. The bristles surrounding the mouth may help the birds to gather up insects as they fly. The dark brown eye is relatively large, a feature which allows for good vision, even when foraging around dawn and dusk, when light levels are low. The striking white lines above and below the eye contrast markedly with the rest of the plumage. Males, like this bird, have chestnut ear-coverts, whereas in females they are green.

[*Hemiprocne comata major*,
Zambales Province,
Luzon, Philippines.
Photo: Doug Wechsler/
VIREO]

as it also reaches perhumid parts of Sri Lanka and similar places elsewhere. The Grey-rumped Treeswift demonstrates the ecological breadth virtually of the whole family in the range of vegetation types occupied, from mature mangroves to evergreen hill forest at 1000-2000 m. All the larger species, nevertheless, very definitely prefer edge habitat, sallying partly over continuous canopy but just as often over open ground, and seemingly dependent on the interface between high canopy and gaps for their home sites. The Crested and Grey-rumped Treeswifts, and probably also the Moustached, reach some of their highest local population densities in mature parkland, forest fragmented by agriculture and, in the case of the Crested Treeswift, groves or gallery woodland actually in savanna country. All three also show a clear preference for perching in bare and exposed parts of the upper crown, from which they have an uninterrupted view of local airspace and, no doubt, of the foraging activity of neighbours. The Whiskered Treeswift also chooses exposed look-outs and nest-sites, but in edge situations typically much further down the vegetation profile, and, unlike the other three, it never hunts over open ground.

General Habits

The treeswifts exhibit bio-mechanical features of both the typical swifts and the swallows, and sharing some of the foraging advantages of these divergent groups imposes a social order that is intermediate between the two, but rather more swallow-like than swift-like. Whereas by breeding and foraging communally most of the typical swifts encountered by treeswifts seem to be trading scarcity of nesting sites for information-exchange on food location, no treeswift has this fitness opportunity at the nest.

The forest-living Whiskered Treeswift is, if anything, more swallow-like than most swallows! Strictly dispersed throughout the year, the pair plus not more than one offspring find food exclusively around a small, apparently unshared activity space. How they defend this space is unknown, and the greater premium may just be on mutual avoidance. A juvenile monitored in Selangor, Malaysia, left the parental territory within weeks of fledging.

None of this species' three larger relatives, all of which inhabit forest edge rather than the interior forest, has been well studied away from the nest, but all seem to have gained something of the best of both worlds. Nesting in the open, they are dispersed breeders like the Whiskered Treeswift. Unlike that species, though, neighbours consort when hunting, apparently regardless of the stage of the breeding cycle. Should only two or three pairs meet, each could still gain a foraging advantage from the communal searching of some collective space for what could be patchy food even for a dietary generalist. It is worth noting here that the extent to which any treeswift specializes in the food it takes has yet to be determined.

As breeding for the year draws to a close, so sociality among the larger species increases. The age-groups participating are unknown, but stable parties can assemble alongside breeders. Thus, a noisy pack of Grey-rumped Treeswifts, presumably including parents, is on record as accompanying the first flights of a late fledgling. Parties of this species also mob Asian falconets (*Microhierax*), which, to judge from their regular hunting behaviour, are liable to be predators of nestling treeswifts.

Outside the breeding season, the three larger species tend to shift ground. How far this applies to established pairs is unknown, but reports of the periodic abandonment of nesting areas apply to all. Rather little is known about this aspect of the Crested Treeswift's biology. Non-breeding Grey-rumped Treeswifts, however, regularly gather in parties of up to 50 birds and occupy a communal home tree at the edge of forest or in semi-open country, including casuarinas at the shore, for several winter months at a stretch, returning to the same tree season after season. No directly comparable behaviour has been recorded for the Moustached Treeswift, but mobility and communal foraging are a normal part of the life of this largest species too. An astonishing 2000 or so individuals reported over a highland valley in western Papua New Guinea would be in line with some fairly spectacular socializing.

Voice

The two crested species, in particular, have a limited repertoire of rather powerful, hysterical-sounding squeals, given freely in

The Crested Treeswift is notable for a distinctive forward-pointing crest, which is often raised, especially as a signal when other birds are perched close by. This species may most easily be distinguished from the very similar and closely related Grey-rumped Treeswift (*Hemiprocne longipennis*) by the fact that its tail streamers project well beyond the tips of the folded wings.

[*Hemiprocne coronata*,
Yala National Park,
Sri Lanka.
Photo: Joanna Van Gruisen/
Ardea]



social contexts: while wheeling and soaring; accompanying a newly flying youngster; or mobbing a predator. Arriving foragers are similarly greeted by a waiting mate or, as non-breeders, by a ragged chorus of neighbours around the home perch.

The vocalizations of the Crested and the Grey-rumped Treeswift are more or less identical. They include a screaming "kee" or "kia", given singly or in a series; a disyllabic call, the main flight-call, variously rendered as "ti-chuk", "whit-chuk", "kee-kik" or "chwe-chwep"; and, commonly in a greeting chorus, a trisyllabic "kip-KEE-kep" or "ki-KEE-kik", stressed heavily on the middle note. The calls of the Moustached Treeswift, also given socially, including in flight, are a high-pitched, downslurred squeak or squeal, "kiiee" or "whiiee"; a softer, upslurred whistle, "owi-wi-wi-wi"; and a loud flight-call, "wick", likened to the call of a sparrowhawk (*Accipiter*).

Whiskered Treeswifts are generally quieter than their larger, more social relatives, and their calls are less well described. Communications between pair-members, perched and in flight, include a high-pitched "chew" or "kweeo" and peal of shorter notes, "kwee kwee, kwi-kwi-kwi-kwi", as well as a "she-she-she-SHEW-she". In this last series, the stressed syllable is pitched higher, as is the case with the crested species.

Food and Feeding

Although arthropods appear to constitute the diet, very little is known of what specific prey treeswifts do actually catch. There is no information at all for the Whiskered Treeswift; a mention only of termites and bees for the Grey-rumped; records of bugs, beetles and small flies for the Crested; and reports of bugs, beetles, bees and ants for the Moustached. No quantitative data are available on the diet of any species. Furthermore, how treeswifts and "true" swifts cope with bee venom is not understood, and the Moustached Treeswift is also reported to take bugs of the family Pentatomidae, another group of insects equipped with good chemical defence.

Among the typical swifts, the known dietary specialists are all medium-sized to relatively big, fast-flying birds covering large distances per foraging day. By contrast, the treeswifts, being tied socially to the crown of a home tree, of necessity exploit a relatively limited and more or less fixed amount of airspace daily, and over long periods. On theoretical grounds, they have a need to hunt opportunistically, taking a good range of whatever comes by that is within handable and energy-efficient prey-size limits. Flexibility of flight mode, from virtually swallow-like manoeuvring up to the fast-forward pace of a big typical swift, pre-adapts the larger species to such a diet, obtained at foraging heights commonly shared with several individually less versatile species of swallow and typical swift. In comparison, the small for-

aging space (often not more than two or three large tree crowns) utilized by a pair of Whiskered Treeswifts specialized in delicate manoeuvring is shared extensively with only one other, still smaller, aerial insectivore, the Glossy Swiftlet (*Collocalia esculenta*).

Typically, prey are taken on the wing, although it seems likely that close in to canopy surfaces the Whiskered Treeswift picks off the occasional food item perched or hanging from the tips of exposed foliage, as also do small apodid swiftlets in these situations. The larger species, at least, forage more intensively in the early mornings and late evenings than at other times, and the Moustached Treeswift is recorded as making the occasional sally even after dark. All treeswifts also tend to be active after rain.

Breeding

No specific sexual display flight has been described for any species of treeswift, although noisy soaring by the larger species is likely to have some social meaning, as yet uninvestigated. An instance of in-flight copulation by the Grey-rumped Treeswift is on record from Sulawesi: the male on top, with wings fully extended, and the partners holding together for about 3 seconds, calling loudly throughout. On the other hand, at least two independent descriptions exist of Moustached Treeswifts copulating on a perch.

The overall breeding seasons of all the species are long. Where adequate information is available, they show a peak of activity in spring or early summer, or twin peaks. There tends to be a break only from late autumn to the beginning or middle of winter, timed according to hemisphere and probably with local variations.

As with the typical swifts, both pair-members co-operate in nest building. They develop the rim of the nest with strands of saliva into which they embed thin flakes of bark, body feathers and small fragments of bryophyte before the solution hardens. The body feathers used are probably mostly, but not exclusively, their own. The Whiskered Treeswift has been shown to add saliva and feathers after laying, and actually while incubating, but the final shallow structure appears only just large enough to contain the single egg, standing proud of the rim like a rather large acorn in its cup.

The nest varies in size according to species, but is only 25-40 mm across at its longest diameter. It sits atop or, more often, forms a hemispherical bracket off the side of a typically narrow, bare twig. Invariably, this twig, often pencil-thin, is fully exposed at the edge of the canopy, giving uninterrupted flight access in most directions. The thinness of the support must help with perching, but may also aid in detecting the approach of a climbing predator. Snakes are active mainly at night, and sleeping on long, thin wands is one of the regular anti-snake strategies adopted by small birds of many kinds which roost in tropical forest.



The Grey-rumped Treeswift shows certain differences from the Crested Treeswift in terms of habitat preference: while the former inhabits evergreen forest, the latter tends to be found more often in deciduous trees. As its vernacular name suggests, the Grey-rumped Treeswift has a noticeably pale greyish rump. Both tend to be found at the edges of forest, and they may have benefited in some areas from disturbance to the denser original forest.

[*Hemiprocne longipennis*
harterti,
Ayer Keroh, Malaysia.
Photo: Ong Kiem Sian]

By day, an empty and unattended nest, seen from a distance, passes for a small, natural woody excrescence, but the plain white egg, often as broad as or even broader than the supporting twig, is by no means cryptic. Treeswift eggs are not well represented in museum collections; indeed, comparative data have been obtained on only two of the four species, the Crested and the Grey-rumped Treeswifts. The shape of these eggs varies from rather broad to a distinctly long, regular oval; the colour from plain white, as also given in all field accounts of the Whiskered Treeswift egg, to the palest shade of grey; and the surface texture from matt to occasionally very slightly glossy. Twelve eggs of the Crested Treeswift measured roughly 23-26 x 15.5-19 mm, while a smaller sample of six Grey-rumped Treeswift eggs measured 23-24.5 x 17-18 mm; the approximate measurements of single Whiskered and Moustached Treeswift eggs were 20 x 15 mm and 30 x 20 mm respectively.

The egg of the Crested Treeswift is said to be gummed to the nest, and it is hard to see how any treeswift egg could survive long on a twig swayed by breeze were it not fixed down. Whether this securing of the egg is by a deliberate act of the parent or is incidental to the moistening and drying of the nest "cement" has not been established.

The orientation of the incubating or brooding adult varies according to the position of the nest on its support, and the latter's thickness. Typical brackets on thin twigs are completely tented by the parent's lower-breast and belly feathering as it perches crosswise on the support, facing and straddling the nest, and a bird incubating in this position cannot be distinguished from one merely resting. A Whiskered Treeswift pair has been seen to leave an egg unattended for several minutes, but a typical incubation relief schedule, recorded in this and the Crested Treeswift, exposes the egg only momentarily. Field observations on nests of these two species reveal that the share of incubation duties taken by females is two or three times greater than that of their mates.

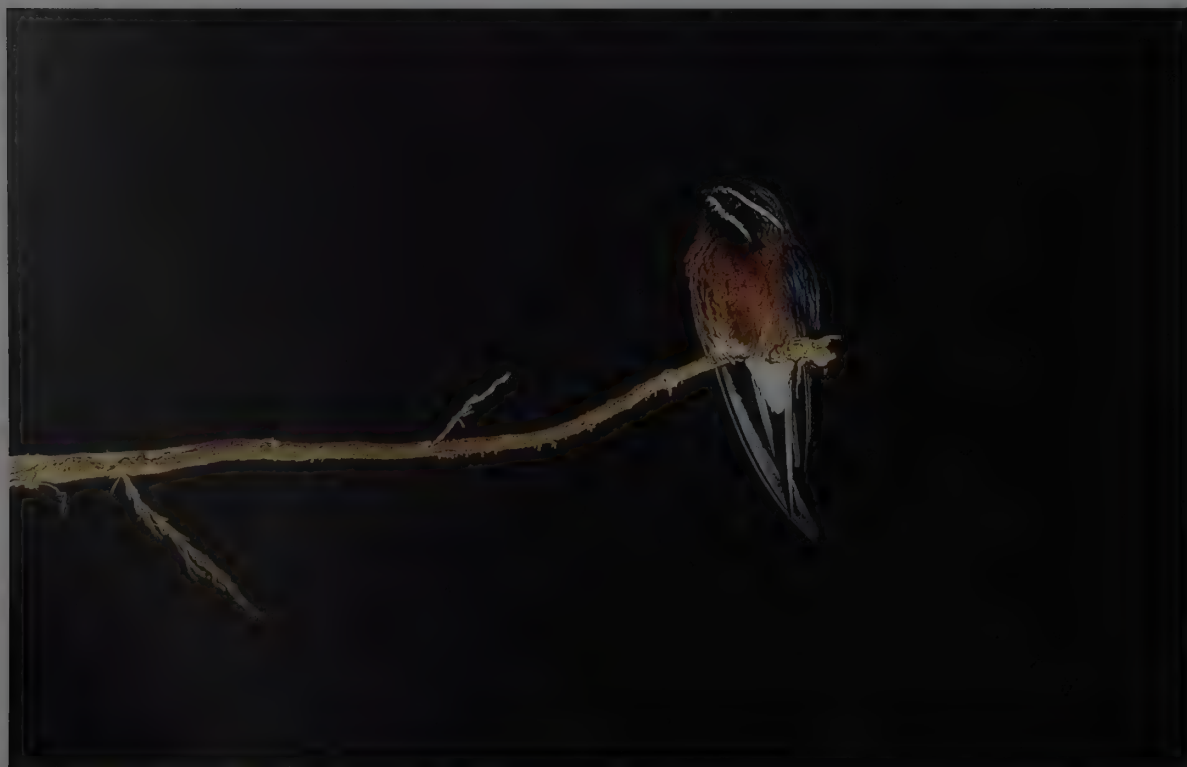
No exact measurements have been made of the incubation and fledging periods, but a Malaysian egg of the Whiskered Treeswift hatched on or before day 21 and the chick flew soon after its 28th day, being fed by both parents at least occasionally for a minimum of three more weeks. At the opposite end of the size spectrum, incubation and fledging of the Moustached Treeswift together occupy more than 60 days.

As with typical swifts, the young treeswift chick is fed a bolus of food, regurgitated from the parent's throat into its open mouth. Later, it takes this food direct from the parent's mouth. A Whiskered Treeswift chick was fed from its first day of life, and within a short time of hatching.

On hatching, the chicks have grey skin and sparse grey down, although descriptions of young Grey-rumped and Moustached Treeswifts suggest that, when dry, they may be fairly well covered. Two or more weeks before flight, the developing chick outgrows the nest, and about the time when its first contour feathers begin to erupt it transfers to the nest support. In all four species this juvenile plumage is cryptic, and remarkably different from that of the adult. In-the-hand descriptions exist for all except the Whiskered Treeswift. The wings, their coverts and the tail are sooty-black, boldly fringed and tipped white to rufous-cream, according to species; the cap and upper body are black, broadly fringed white, cream-buff or, commonly in the Moustached Treeswift, rufous, in addition to which the cap feathering is subapically zoned buff, dark brown and/or rufous. Non-black zones take over to give a pale forehead and lateral coronal bands in the Crested Treeswift, and in the stripe-faced species an incipient supercilium and malar streak are evident. The tertial patch, white in adults, shows buff, typically with a subapical band of dark brown. The underpart feathers are pink-buff with an outer zone of dark brown and a white fringe; or, in the Moustached Treeswift, like the upperparts down to the breast, then buff with bands of black, rufous and white. The colours and the entire coarse, mealy pattern simulate lichen-covered bark, this effect enhanced by the behaviour of the chick when unattended: sitting rigidly upright with head tipped to align the bill, and with the otherwise contrastingly dark eye closed, it passes off easily as a small branch stub.

Movements

No treeswift migrates in the regular sense, and the forest-living Whiskered Treeswift is strictly sedentary, remaining in its nesting territory all year round. Seemingly erratic comings and goings imply that the Moustached Treeswift may be nomadic in parts of its range, but the scope of individual journeys may not be more than local. While there is the contrary indication of a

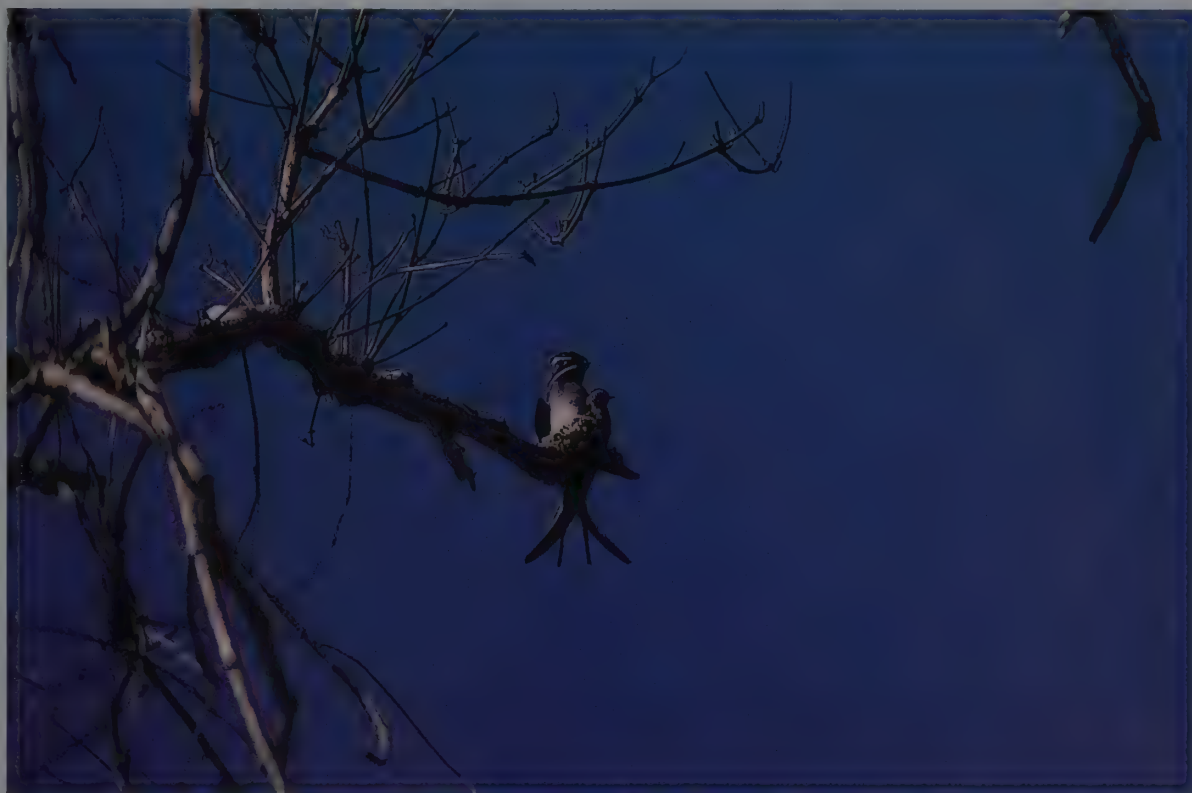


The Whiskered Treeswift is small and light, and well able to perch even at the tips of thin twigs, as it waits between feeding forays. Treeswifts also roost in such situations, which probably offer them an extra degree of safety from non-flying predators, such as snakes. Of all the treeswifts, this species is tied most closely to natural forests, and it is seen much less often in parks, orchards or plantations. Unlike the other treeswifts, it prefers to perch and hunt in amongst the branches and twigs of the forest trees, rather than venturing into the open skies above the forest canopy.

[*Hemiprocne comata*
comata,
Sabah, Borneo.
Photo: Sarah Whitley]

Treeswifts build tiny nests from feathers, bark and leaf fragments, glued together and onto the top of a branch using saliva. The nest is often hard to spot, as it may be situated high in a tree, and looks like part of a branch. The nest is rather fragile, with thin, papery walls, and is only just big enough to hold the single egg. It is unable to support the adult, or even a large chick; indeed, this Moustached Treeswift chick has outgrown its nest. The adult incubates the egg by squatting on the branch, at which time it completely hides the nest from view with its body. Clearly visible here are the scythe-shaped wings, which cross over when the bird is at rest, and the streamers of the deeply forked tail.

[*Hemiproctes mystacea*
mystacea,
Veimaure River,
south-east New Guinea.
Photo: Brian J. Coates]



casualty recovered from the permanent snow zone of the Carstensz Mountains in Irian Jaya, a good 3000 m above terrain regularly used by the species, this one-off record is backed by no other evidence.

Both the Crested and the Grey-rumped Treeswifts shift seasonally, possibly only locally, although the size of some winter gatherings of the latter species in the Malay Peninsula leads one to conclude that these may draw recruits from a fairly wide range. It has not yet been shown whether such gatherings include full adults, although year-to-year usage of favoured trees implies that they probably do.

Relationship with Man

Rather surprisingly for noisy, visible birds which often live on the outskirts of villages, there appears to be very little information on the attitudes of humans towards treeswifts in their native countries. Indeed, no cultural or economic links are known between these birds and local human populations. It is tempting to suggest that treeswifts are "welcomed" because they are clearly insectivores, consuming rather large quantities of insects which might be considered potentially injurious pests, but there is no definite evidence that this is the case. Whatever the motivations, it appears that treeswifts and man generally co-exist, with limited direct contact and no regular conflict.

Given access to high perches and nest-sites, treeswifts, including the forest-dwelling Whiskered Treeswift, are not put off by regular human traffic nearby, appearing to rely completely on the security provided by their resting perches and nests from terrestrial predators. That treeswifts have little fear of man is nicely illustrated by the following account. In 1939, the eminent ornithologist E. H. N. Lowther described the boldly confiding behaviour of a pair of Crested Treeswifts near Dhanbad, in Bihar, east India. The two birds continued their nesting duties as normal while he photographed them from a hastily built platform, in full view and at no more than arm's length from the nest. On only the second day of his observations, the female allowed him to ruffle her feathers, and grappled with an offered finger as she incubated. In order to see the contents of the nest, Lowther had actually to push the sitting adults off it.

Status and Conservation

While hunting partly over the canopy of continuous forest, most treeswift species select home trees to which they return between sorties. These trees are situated where forest meets open space. Over much of the family range, windthrow clearings and river courses would have been almost the only available edge habitat, until conditions were vastly extended along expanding systems of roads and around settlements and agriculture. Forest-bound Whiskered Treeswifts respond to space opened up along log-extraction tracks and other small roads, while all the larger species have actively spread into cultivated landscapes, including even the planted timber of gardens and parks. Some of the densest local populations of, for example, the Grey-rumped Treeswift are actually in these latter types of situation.

No treeswift species could survive total clearance of tall trees, and none occurs in oil palm monoculture, the crop now most extensively replacing forest throughout the humid lowlands of the family range. All, however, appear likely to have benefited from the intermediate fragmentation of continuous forest cover. Over their entire range, at present, all treeswifts are regarded as common birds, although the Whiskered Treeswift is as vulnerable to outright habitat loss as is the rest of its community: not yet under direct threat, but a species to be watched.

The collapse of the Grey-rumped Treeswift population in Singapore, as measured by a decline in the size of non-breeder gatherings, has no immediately obvious connection with availability or quality of habitat there. The unusual scarcity of certain other typical swift species there compared with the nearby mainland points more directly towards a problem with aerial plankton and, ultimately, pesticides. In western Indonesia, most seriously Java, random hunting of all birds has become a problem for the conservation of non-forest populations of the Grey-rumped Treeswift.

General Bibliography

Bock (1994), Chantler (1995c), Chantler & Driessens (1995a), Holmgren (1998), Karkhu (1998), Lack (1956b), Lack & Collins (1985), Lucas (1889, 1895), Orr (1963), Peters (1940a), Sibley & Ahlquist (1990), Sibley & Monroe (1990), Sibley *et al.* (1988), Smythies (1968), Waugh & Hails (1983).



PLATE 44

Family HEMIPROCNIIDAE (TREESWIFTS)
SPECIES ACCOUNTS

Genus *HEMIPROCNE* Nitzsch, 1829

1. Crested Treeswift
Hemiprocne coronata

French: Hémiprocne couronné

Spanish: Vencejo Arborícola Coronado

German: Kronenbaumsegler

Other common names: (Indian) Crested Swift

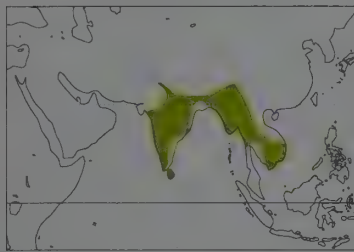
Taxonomy. *Hirundo Coronata* Tickell, 1833, Borabhum and Dhalbhum, Bihar-Bengal border, north-east India.

Forms a superspecies with *H. longipennis*, with which it has been considered conspecific: morphological differences are constant, however, with no evidence of intergradation where parapatric ranges of the two meet. Monotypic.

Distribution. Sri Lanka, India (W to N Uttar Pradesh and SE Gujarat), S Nepal and S Bhutan to Myanmar, SC China (SW Yunnan), NC & W Thailand (S to Kaeng Krachan) and S Indochina.

Descriptive notes. 23-25 cm. Adult has crest dark greenish-blue, 2.5-3 cm tall. Male uniformly pale greenish-grey from central crown to uppertail-coverts; lores black, finely bordered white above; anterior ear-coverts, lower face, chin and variable extent of throat rufous; wing-coverts glossy greenish-black; underwing-coverts pale grey, concolorous with breast and flanks, and belly and undertail-coverts whitish. Differs from *H. longipennis* in tail-streamers projecting well past folded wing-tips. Female lacks rufous on face, has grey-black ear-coverts and cheeks, white moustachial stripe and grey chin and throat. Juvenile a finely banded mixture of sooty-black, rufous, buff and white, predominantly dark above, with pale forehead and lateral coronal band, and white spot in front of eye.

Habitat. Scattered trees, groves, and edge and canopy breaks of more or less continuous, fully to mainly deciduous forest (dry dipterocarp, teak, etc.); also tall secondary growth and, marginally at



Indian Subcontinent, becoming bimodal (Mar-May and Jul-Sept) in Sri Lanka, and recorded Mar-Jun in Myanmar. Nesting dispersed, but several pairs may occur in the same general area. Nest a half-saucer of hardened saliva incorporating small, sometimes overlapping flakes of bark and body feathers, c. 12 mm thick and built as a bracket 20-30 mm wide, 4-18 m up on a live, usually thin branch in open canopy. Lays 1 egg, which is glued to the nest; incubation by both sexes, period unrecorded; nestling down grey; chick is brooded more or less continuously through the down-plumage stage, and fed by both parents; fledging period unrecorded, but appears to be longer than 4 weeks.

Movements. Mainly resident; seasonal dispersive movements are perhaps only local; records from Bangladesh may refer to vagrants or to rare resident population.

Status and Conservation. Not globally threatened. Patchily distributed and often local, but relatively common, and able to live close to human activity; rare in Bhutan, Bangladesh and NE India. Selection of edge habitat and capacity to use tall secondary growth suggest that it may have benefited from moderate forest disturbance. Under serious threat only in those areas where clearance has reached the point of severe tree loss.

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2. Grey-rumped Treeswift

Hemiprocne longipennis

French: Hémirocné longipenne

Spanish: Vencejo Arborícola Culigrís

German: Haubenbaumsegler

Other common names: Crested Treeswift(!)

Taxonomy. *Hirundo longipennis* Rafinesque, 1802, Java.

Forms a superspecies with *H. coronata*, with which formerly sometimes treated as conspecific. Several races have been described, but most nowadays considered invalid, e.g. *ocyptera* (Nias I), *thoa* (Batu Is, Pagi Is, Enggano I) and *anochra* (Natuna Is). Four subspecies recognized.

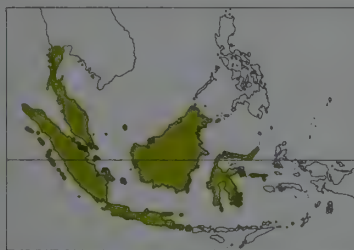
Subspecies and Distribution.

H. l. harterti Stresemann, 1913 - S Myanmar (S Tenasserim) and SW Thailand S & E to Sumatra, Borneo and intervening islands, and Sulu Archipelago E to Tawitawi (Philippines).

H. l. perlonga (Richmond, 1903) - W Sumatran islands from Simeulue to Enggano.

H. l. longipennis (Rafinesque, 1802) - Sunda Strait (Panaitan I) through Java to Lombok, and Kangean Is (E Java Sea).

H. l. wallacii (Gould, 1859) - Sulawesi, including S and E satellites, and Sula group (W Moluccas).



but dorsal patterning often more complex, particularly on cap, which lacks contrasting lateral band, and has no obvious pale loreal spot. Races *harterti* and *perlonga* shade darker than nominate on anterior underparts, and rump less pale in relatively large *perlonga*; *wallacii* largest, with plumage much as nominate.

Habitat. Groves of large trees and edge and canopy breaks of more continuous semi-evergreen and evergreen forest inland, locally tall mangroves and coastal casuarinas, also making use of tall plantation and mature parkland trees. Everywhere selects well-exposed, bare perches at outer edge of the high canopy. From plains level to 1200 m in Malay Peninsula, to 1550 m in Java.

Food and Feeding. Flying arthropods; prey selection hardly known, but regularly attends swarms of alate termites and, in Borneo, recorded taking bees from the edge of a flying swarm. Prey caught during long sorties out from a favoured tree crown, typically well clear of vegetation surfaces. In Selangor, Malaysia, mean foraging height above open ground was 35 m, and above forest canopy was 47 m. Like other Apodiformes, drinks by scooping water in a fast, skimming swoop down to an open surface.

Breeding. In N Hemisphere, laying season overall Feb-Aug/Sept (chick records in Oct), peaking in Mar-Jun; in S (Java) active nests Dec-Aug. Nesting dispersed but, as with *H. coronata*, often with several other pairs in the neighbourhood. Nest as that of *H. coronata*, built by both sexes, typically a half-saucer of hardened saliva incorporating small scraps of moss, bark flakes and body feathers, c. 36 x 24 mm, maximum outside depth 12 mm, built out as a bracket 5-30 m up on a thin, exposed branch. Lays 1 egg; both pair-members incubate and both tend the chick; incubation and fledging periods not recorded; chick down is grey.

Movements. Breeds over its whole altitudinal range, with probably no more than post-breeding local dispersive movements.

upper limit of range, semi-evergreen forest. Selects bare, exposed perches on outer surface of the canopy. From plains level to about 1300 m in Indian Subcontinent, to 1400 m in SE Asia.

Food and Feeding. Flying arthropods; diet said to include hemipteran bugs, beetles and small flies, but hardly analysed and proper details are lacking. Captures prey during long sorties out from high perches into free space clear of vegetation surfaces, including well above the forest canopy.

Breeding. Season Dec-Oct overall, with regional variation: peak activity Jan-Apr in

Status and Conservation. Not globally threatened. More or less common through most of its range, and under no serious threat overall. As with *H. coronata*, preference for patchy tree cover and edge habitat over continuous natural forest suggests that it may in fact have benefited from some forest disturbance; the species is absent, however, from still rapidly expanding oil palm agriculture, and populations in the plantation landscape would benefit from a commitment to the maintaining of natural or semi-natural shelterbelts. The opposite trend is set in Malaysia, where over-use of organophosphate pesticide sprays in suburban parkland habitat is another rising issue. Pesticides are suspected to be behind a recent population decline in Singapore. Elsewhere, the general impression is that bird-hunting, exacerbated by expanding availability of airguns, will have damaged non-forest populations through much of W Indonesia; hunting has caused quite severe reduction of nominate race, along with nearly all bird species, in lowland Java.

Bibliography. Allen (1952), Bishop (1992), Bromley (1948), Brooke (1969e), Brooks & Dutton (1997), Bucknill & Chasen (1990), Coates & Bishop (1997), Coomans de Ruiter (1935), Dickinson *et al.* (1991), Duckworth & Kelsh (1988), Duckworth *et al.* (1997), Dymond (1994), Eck (1976), Gibson-Hill (1950b), Glenister (1951), Hails & Jarvis (1987), Hellebrekers & Hoogerwerf (1967), Holmes, D.A. (1994a), Holmes, D.A. & Burton (1987), Holmes, D.A. & Philipps (1996), Hoogerwerf (1965), Inskipp *et al.* (1996), Johnstone *et al.* (1993), Lekagul & Round (1991), MacKinnon (1988), MacKinnon & Philipps (1993), Madoc (1976), van Marle & Voous (1988), Medway & Wells (1976), Mees (1986), Nash & Nash (1988), duPont & Rabor (1973a), Riley (1938), Robertson (1993a), Round (1988), Smythies (1981, 1986), Somadikarta (1975b), Stones, Lucking *et al.* (1997), Vowles & Vowles (1984), Wardill (1995), Watling (1983), Wells (1999), White & Bruce (1986), Wilkinson *et al.* (1991).

3. Whiskered Treeswift

Hemiprocne comata

French: Hémirocné coiffé

German: Ohrenbaumsegler

Spanish: Vencejo Arborícola Chico

Other common names: Lesser Treeswift

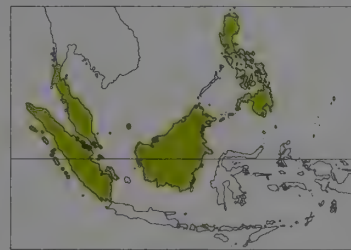
Taxonomy. *Cypselus comatus* Temminck, 1824, Sumatra.

Additional races proposed for some of islands off W Sumatra (*stresemanni*) and for some of Philippines (*nakamurai*), but both now considered invalid. Two subspecies currently recognized.

Subspecies and Distribution.

H. c. comata (Temminck, 1824) - S Myanmar (S Tenasserim) and peninsular Thailand S to Sumatra (including W Sumatran islands) and Borneo and intervening islands.

H. c. major (Hartert, 1895) - Philippines, including Sulu Archipelago, but excluding Palawan.



Descriptive notes. 15-17 cm. Only slightly crested. Male mostly dark bronze, with bold supercilium from forehead and lores to hind-nape and a more or less parallel stripe from chin back to side of neck, both sharply white against otherwise glossy black head and throat; lower ear-coverts dark chestnut. Female similar, but ear-coverts deep blue-green. Juvenile finely barred brown, tawny, grey and white, much as congeners; whitish facial stripes shorter than in adult. Race *major* has more white on abdomen and tertials, broader, blunter, more juvenile-like tail-streamers, and proportionately shallower tail-fork; also averages

larger, but Sumatran and Malay Peninsula birds both increase in size clinally northwards, giving much overlap between races.

Habitat. Small cover breaks and the main canopy of evergreen forest inland, and locally also of tall, mature mangroves. From plains level up to 1000-1100 m on major slopes, but not above 800 m in N Malay Peninsula.

Food and Feeding. Small flying arthropods, but diet not analysed. Compared with typical behaviour of co-occurring *H. longipennis*, forages from perches further down the canopy profile, taking prey in much shorter sorties close to vegetation surface; never above main canopy height.

Breeding. Over most of range lays Feb-Aug (latest fledglings in early Oct); the few Philippine records, dated only May. Nesting dispersed and breeding pairs territorial. Nest a half-saucer of hardened saliva incorporating feathers, but no published confirmation of vegetable matter included; built 8-40 m up as a bracket or on upper surface of a thin, exposed branch; construction continues after laying. Lays 1 egg; both pair-members incubate and tend the chick; natal down colour not described; in one instance, an egg hatched on or before day 21 and the chick flew soon after day 28, giving total development time of probably not less than 50 days.

Movements. Sedentary; breeding pairs are believed to remain in their nesting territory throughout the year.

Status and Conservation. Not globally threatened. Reported as common in most parts of range; very few recent records from Singapore. Tied more exclusively to original forest, hence at greater risk of outright habitat loss, than others of genus. Exceptional in secondary growth, but able to exploit edge created by selective logging.

Bibliography. Bucknill & Chasen (1990), Danielsen *et al.* (1994), Delacour & Mayr (1945, 1946), Dickinson *et al.* (1991), Duckworth & Kelsh (1988), Duckworth *et al.* (1997), Evans, Dutton & Brooks (1993), Gilliard (1950a), Gonzales (1983), Holmes, D.A. (1994a), Holmes, D.A. & Burton (1987), Lekagul & Round (1991), MacKinnon & Philipps (1993), Madoc (1976), van Marle & Voous (1988), McClure (1979), Medway & Wells (1976), Mees (1986), Nash & Nash (1988), Neumann (1937), Parkes (1960a), duPont & Rabor (1973a), Rabor (1977), Rand & Rabor (1960), Riley (1938), Robinson & Kloss (1924), Robson & Davidson (1996), Round (1988), Salomonsen (1983), Sharpe (1879a), Shefford (1916), Smythies (1981), Verheugt *et al.* (1993), Vowles & Vowles (1984), Wells (1999), White & Bruce (1986), Wilkinson *et al.* (1991).

4. Moustached Treeswift

Hemiprocne mystacea

French: Hémirocné à moustaches

Spanish: Vencejo Arborícola Bigotudo

German: Bartbaumsegler

Other common names: Whiskered Treeswift(!)

Taxonomy. *Cypselus mystaceus* Lesson, 1827, Dorey, Vogelkop, Irian Jaya.

Six subspecies recognized.

Subspecies and Distribution.

H. m. confirmata Stresemann, 1914 - Moluccas (excluding Kai and Sula groups) to Aru Is.

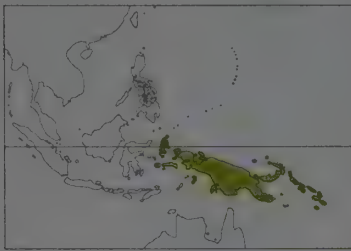
H. m. mystacea (Lesson, 1827) - New Guinea mainland; islands of Geelvink Bay and W Papuan Is.

H. m. aeroplanes Stresemann, 1921 - Bismarck Archipelago (excluding Admiralty Is and Feni Is).

H. m. macrura Salomonsen, 1983 - Admiralty Is.

H. m. woodfordiana (Hartert, 1896) - Feni Is and most of Solomon Is (including Bougainville).

H. m. carbonaria Salomonsen, 1983 - Bauro I (Solomons).



Descriptive notes. 28-31 cm; 56-79 g. Only slightly crested. Male has two bold white facial stripes contrasting with glossy black cap and black face, with lower ear-coverts variably dark chestnut; rest of body blue-grey, paler below, with usually white central belly to undertail-coverts. Female differs only in having dark blackish-green ear-coverts. Juvenile head and body feathers complexly zoned black, rufous, buff and white, generally black-based dorsally and anteriorly, with cream-rufous forehead, lateral coronal bands and malar stripes, and with rear underparts cream-based. Races differ mainly in size and in body colour:

all others smaller than mainland nominate, *confirmata* otherwise similar; *aeroplanes* and *macrura* have less white on vent, latter also particularly long-tailed; *woodfordiana* and *carbonaria* smallest and with uniformly dark body.

Habitat. High emergent crowns in mangroves and beach-strand woodland, scattered trees and groves, and edge of inland forest (gallery forest in savanna areas) overlooking open country and along rivers that broadly break the canopy. From sea-level to 1580 m; a casualty recovered from ice at 4400 m in the Carstensz range.

Food and Feeding. Takes flying arthropods, including bees, ants, hemipteran bugs and beetles, in length range 6-18 mm. As is typical of the family, forages from bare, exposed perches at the top or

outer edge of canopy; launches often-long sorties into free airspace, including well above the canopy, returning each time to the favoured crown

Breeding. Active nests recorded in all months except Mar; season locally variable, can be long. Nesting is dispersed, and pairs believed to be territorial, at least around the nest-site. Nest a tiny saucer of feathers and plant material incorporated in hardened saliva, fixed on the top of a high, horizontal branch (no bracket nest described); simulates a small knot and, as with congeners, is completely hidden by the sitting adult. Lays 1 egg; both sexes incubate, but most brooding of the young chick is by female; combined incubation and fledging period in excess of 60 days. A record of possible second brood, at same nest, in Port Moresby area.

Movements. Locally dispersive resident, but perhaps nomadic in some areas; movements little studied.

Status and Conservation. Not globally threatened. Relatively common generally, with no hint yet that any race is threatened, although some individual Wallacean island populations may be under pressure. The mainland New Guinea range still carries an immense extent of suitable habitat, and the species' capacity to use broken landscape suggests that, except possibly in some W islands, it can withstand much more damage to forest than has occurred to date. On the other hand, no information exists on how it responds to plantation agriculture, which is the future of the lowlands of the region. In Irian Jaya widespread settlement of W Indonesian transmigrants will greatly increase the level of bird-hunting, a traditional activity of these people.

Bibliography. Bailey (1992), Beechler (1978), Beechler *et al.* (1986), Bell (1986), Bishop (1978, 1992), Blaber (1990), Bowler & Taylor (1989), Buckingham *et al.* (1995), Burrows (1987, 1993), Cain & Galbraith (1956), Coates (1985), Coates & Bishop (1997), Dahl (1899), Diamond (1972), Eastwood (1989a), Finch & McKean (1987), Gregory (1995a, 1995b), Hadden (1981), Halliday (1992), Isherwood *et al.* (1997), Jepson (1993), Jones & Lambley (1987), Majnep & Bulmer (1977), Mayr (1936), Mees (1965, 1982a), Meyer (1928), Palliser (1989), Rand (1942a), Rand & Gilliard (1967), Ripley (1964a), Salomonsen (1983), Schodde (1977), Schodde *et al.* (1975), Storer & Eastwood (1991), Tolhurst (1991), Wahlberg (1988), White & Bruce (1986).

Class AVES
Order APODIFORMES
Suborder TROCHILI
Family TROCHILIDAE (HUMMINGBIRDS)



- Small to tiny fast-flying birds, with extensively iridescent plumage, many with strikingly coloured gorget or crest; thin bill extremely variable, from short to extremely long, from straight to sharply curved; feet tiny.
- 5-22 cm (with tail streamers, up to c. 35 cm).



- New World, mainly Neotropical.
- Wide variety of habitats, wherever suitable food plants occur, from sea-level up to c. 5000 m, with greatest diversity in submontane zone.
- 102 genera, 328 species, 684 taxa.
- 25 species threatened; 1 definitely extinct since 1600.

Systematics

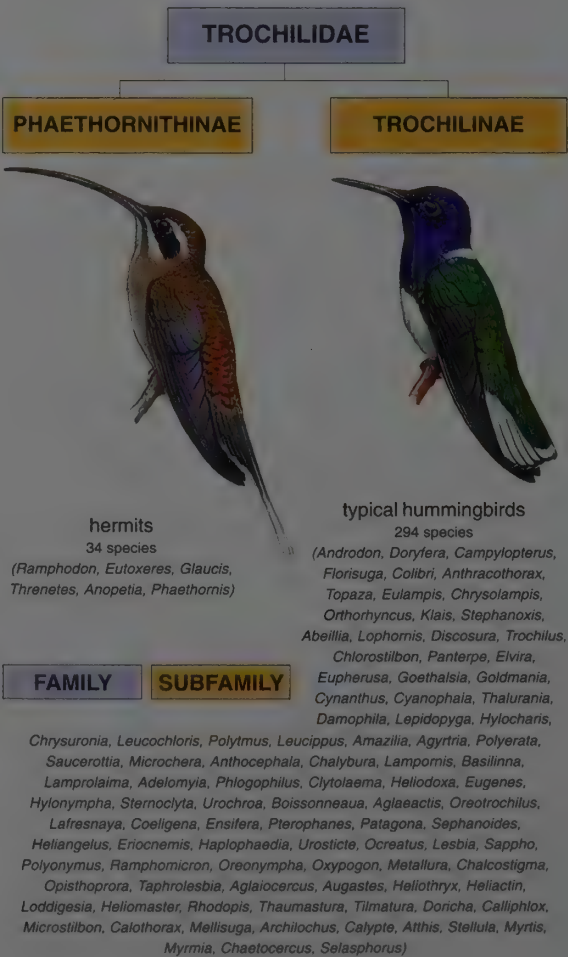
Hummingbirds (Trochilidae), with some 328 recognized species, are one of the largest avian families in the New World, surpassed in species number only by the tyrant-flycatchers (Tyrannidae) with over 370. Although hummingbirds form an undisputed phylogenetic unit, their sister-group relationship is still debated. Traditionally trochilids are placed within the Apodiformes, together with the treeswifts (Hemiprocnidae) and the true swifts (Apodidae). This classification is based mainly on anatomical and morphological characters, such as modified cervical musculature, the skeleton of the flight apparatus, wing muscle innervation, or feather tracts, and the question still remains whether these similarities are due to convergence or to common ancestry. This debate has led some classifiers to place hummingbirds in an order of their own, Trochiliformes.

Recent biochemical studies favour the traditional classification: swifts and hummingbirds share a unique form of the enzyme malate dehydrogenase. This phylogenetic treatment is corroborated by the DNA comparisons of C. G. Sibley and J. E. Ahlquist.

Today, the monophyly of swifts and hummingbirds is widely accepted among ornithologists. The divergence is probably ancient and may date back to the beginning of the Tertiary (c. 65 million years ago) or even to the late Cretaceous (c. 70 million years ago), when a large tectonic plate broke from Gondwanaland, giving rise to South America. The relationship of the apodiforms to other avian groups is the subject of rather controversial debate. Affinities to nightjars and their allies (Caprimulgiformes) based on patterns of feather growth (pterylosis), to mousebirds (Coliiformes) from intestinal tract comparisons, and even to the "pico-passerine assemblage" of the songbirds (Passeriformes), derived from feather structure and egg-white protein analysis, have been suggested by various systematists. Most of the evidence for these links is based on similarities of debatable significance, and not on a common possession of derived characters (synapomorphies) defining monophyletic lineages. Modern anatomical methods, careful morphological character analyses, and molecular biology techniques may in the future shed some light on these unsolved problems of higher-level relationships.

Several attempts to classify hummingbird genera and species have been made since the second half of the 19th century, and indeed most of our present knowledge of systematic affinities within the family dates back to that time. When J. L. Peters

published Volume 5 of the *Check-List of Birds of the World* in 1945, dealing with the Trochilidae, he basically followed E. Simon's classification of the family formulated in 1921. Except for some minor modifications this list is still in use today.



Subdivision of the Trochilidae
(Figure: Hilary Burn)

The hummingbirds are traditionally situated alongside the swifts (Apodidae) and tree-swifts (Hemiprocnidae) in the Apodiformes.

This placement is based on skeletal and muscular similarities, supported by analyses of proteins and genetic material.

The relationship of the Apodiformes to other orders is more obscure, but they have been linked with nightjars and allies (Caprimulgiformes), mousebirds (Coliiformes) and passerines. Within the family, provisional taxonomic adjustments are a constant feature.

The Purple-throated Woodstar, for example, was previously placed in the genus *Philodice* but this has recently been subsumed into the genus *Calliphlox*.

[*Calliphlox mitchellii*,
Valle, Colombia.

Photo: Luis Mazariegos]



Modern phylogenetic studies of hummingbirds have mainly focused on species- and genus-specific questions. Surprisingly little is known about the general relationships within the Trochilidae. There are two major reasons for this: first, the lack of fossil hummingbird records except for a few modern species, mainly from West Indian Quaternary cave deposits; second, most previous classificatory studies concentrated on the analysis of complex morphological variations, or on myological and other anatomical features of only a small number of taxa. Thus, classification attempts often failed because of a lack of holistic background knowledge on functional anatomy, morphology, biogeography and behaviour of the majority of species, leading to phylogenetic misinterpretations due to convergence, parallelism and extreme anagenesis, or evolution towards higher levels of specialization, common phenomena in hummingbirds. Many of the independently evolved structural and functional similarities in trochilids can be explained as adaptations to their highly specialized hovering flight and feeding apparatus, designed to exploit the nectar of angiosperm flowers. Other factors fostering convergence and parallelism are sexual selection pressures on polygamous males by female choice. Thus males of many unrelated species show striking similarities in form and colour of advertisement plumage like crests, gorgets, elongated and variously modified tail feathers, and puff thighs.

Some of the recent studies on hummingbird taxa similarly lack a major prerequisite, namely a sound knowledge of their biogeographical history, allowing the judgement and calibration of character variations within an evolutionary framework. If classificatory studies take account of the evolution of these patterns in time and space, as shown for the Andean *Metallura*, *Chalcostigma* and *Agelaiocercus* complex, the sometimes negatively viewed traditional morphological character analysis may yield valuable information on intraspecific and interspecific phylogenetic relationships, serving as a useful hypothesis to be tested with other methods.

Historically, two subfamilies are generally distinguished within the Trochilidae: the hermits (Phaethornithinae) and the trochilines or typical hummingbirds (Trochilinae). Within these two systematic units, the hermits comprise the six genera *Glaucis*, *Threnetes*, *Ramphodon*, *Eutoxeres*, *Anopetia* (formerly included in *Phaethornis*) and *Phaethornis*, whereas the trochilines form

an assemblage of some 96 genera, which by some authors would be increased to over 100.

Hermits differ from the trochiline hummingbirds by their characteristic humeral tendon and their predominantly pigmentary brownish, greyish and reddish colours. Iridescent colours are sparse and mostly limited to the upperparts. Hermits are generally non-territorial, occur in the understorey of tropical forest or dense scrub, and usually have long bills adapted to flowers with tubular corollas. In all species studied, males gather at leks where they attract females. In their displays, male her-



In 1861, John Gould split hummingbirds into two subfamilies, Phaethornithinae and Trochilinae, and to this day his arrangement stands, mainly for want of consensus on an alternative proposal. The vast majority of species fall into the Trochilinae, a mixed assortment of largely territorial and sexually dichromatic forms. Within this subfamily, the White-bellied Woodstar, belongs in the "starthroat-and-woodstar" assemblage which is linked, amongst other features, by the existence of an eclipse plumage, males often resembling females. This species was previously placed in *Acestrura*, but is now considered to belong in *Chaetocercus*.

[*Chaetocercus mulsant*,
Quindío, Colombia.

Photo: Luis Mazariegos]



Trochilines are generally polygamous, the displays of males often featuring solitary aerial manoeuvres and spectacular plumage traits rather than communal lekking. Within this group, generic limits are poorly understood, a situation highlighted by the fact that around half the trochiline genera are monotypic. With changing taxonomic trends, however, this proportion is gradually declining. The Swallow-tailed Hummingbird, for example, was formerly isolated in *Eupetomena*, but has now been merged with the sabrewings (*Campylopterus*), on the basis of its song structure and the male's thickened primary shafts.

[*Campylopterus macrourus macrourus*, Rio de Janeiro, Brazil. Photo: Luiz Claudio Marigo]

mits employ fanned rectrices and wide-open bills showing the yellow, orange or red interior base of the lower mandible (Gape Display). All known nests of hermits are pendent, often cone-shaped, either attached to the inner tip of a long, narrow, bending leaf or fastened to a vertical root or twig if shelter is provided by a riverbank, cave vegetation, or even a bridge. A recently published careful systematic analysis of these various characters indicates that hermits form a distinct monophyletic group within the Trochilidae.

The more diverse hummingbird subfamily, Trochilinae, is heterogenetic and less distinctive than the hermits. This has led several taxonomists to seek clues allowing further splitting at the subfamily level. For instance, one proposal is to place the coquettes and thornbills in a subfamily, Lophornithinae, and to consider the distinctive members of the genera *Androdon* and *Doryfera* as another subfamily, Doryferinae. Whereas the classification of the Lophornithinae is based mainly on the somewhat superficial location and development of the nasal operculum and the primaries, the Doryferinae are markedly different in their hindneck musculature and song structure from all other previous subdivisions. Systematists agree that the genera *Androdon* and *Doryfera* are not members of the hermit assemblage, to which they were formerly assigned, but their advocated subfamily status should be considered with caution in the absence of detailed comparative anatomical and bioacoustical information. The differences observed in *Androdon* and *Doryfera* may well represent a trochiline-specific early evolutionary state and/or a behavioural adaptation for foraging and communication in forest understorey.

Until our knowledge is improved by further character analyses it seems appropriate to maintain the traditional classification of merely the two hummingbird subfamilies Phaethornithinae and Trochilinae designated by John Gould in 1861.

The Trochilinae comprise about 90% of hummingbird species. They exhibit a trochiline-specific pattern of the humeral tendon. Their often straight to slightly decurved bills range from a few millimetres in the Purple-backed Thornbill (*Ramphomicron microrhynchum*) to 12 cm in the Sword-billed Hummingbird (*Ensifera ensifera*). Most show marked sexual plumage-colour dimorphism. Iridescent bright colours of many metallic shades of red, orange, green and blue frequently occur on the head, upperparts and underparts of males. In some species, jewel-

coloured adornments like expandable gorgets, crests and elongated modified tail feathers are striking male characters. Females are of duller appearance, frequently lacking the brightly coloured feather parts. However, in some species plumage dimorphism is minor or absent, such as in members of the genera *Colibri* and *Eulampis*, where males and females are almost visually inseparable to the human eye. Males of the brightly coloured trochilines are generally territorial; lek behaviour is known only for a few species; and courtship in many non-hermits features characteristic aerial displays. Nests are predominantly cup-shaped and attached to branches or forked twigs, though pendular (*Doryfera*) and domed (*Agelaiocercus*) constructions are known. Trochilines live in extremely diverse habitats ranging from desert borders, mangroves and tropical rainforests to the perennial meadows below the snow-line of high-Andean peaks.

Generic limits and species relationships within the trochilines are still poorly understood. Indeed, many non-hermit genera are based on the same characters that are used to define species. In recent checklists and classifications the lack of synapomorphies at the genus level in trochilines is expressed by over 50% of monotypic genera. All this taxonomic uncertainty presents a considerable challenge for future systematic research.

Despite this problem, several major clades have been identified among the non-hermits. Based on the variation of a single wing muscle, the *Musculus tensor patagii brevis*, three groups within the Trochilinae have been proposed. The first unit covers those genera with a primitive muscle state: *Androdon*, *Doryfera*, *Florisuga*, *Colibri*, *Anthracothonax*, *Eulampis*, *Chrysolampis*, *Polytmus*, *Topaza* and *Heliothryx*. A more advanced muscle state was found in the following genera: *Campylopterus*, *Orthorhynchus*, *Stephanoxis*, *Lophornis*, *Discosura*, *Chlorostilbon*, *Cyananthus*, *Cyanophaea*, *Thalurania*, *Panterpe*, *Damophila*, *Lepidopygia*, *Hylocharis*, *Amazilia*, *Trochilus*, *Lampornis*, and all Andean and North American taxa. The category "highly advanced" muscle state comprises members of the genera *Calliphlox* and *Chaetocercus*.

This single-character arrangement is surprisingly consistent when compared with morphological, morphometric and behavioural information. Using these data sets, eleven distinct taxa can be clustered. Patterns of tail feather coloration, display, and song structure, and a primitive cross-structure feature of the hindneck

While there has been a tendency for some related groups to be merged, other genera have been divided. The best example of this latter phenomenon is the genus *Amazilia*.

Until recently this was considered to consist of a clumsily diverse clade of 28 small species grouped together on account of similarities in nest structure and cervical musculature. Biogeographical analysis suggests that these similarities are superficial and conceal different origins within a polyphyletic assemblage. For this reason *Amazilia* has been split into four separate genera. The six members of the new streamlined *Amazilia*, typified by the Rufous-tailed Hummingbird, have much red in the bill and rufous in the tail. A further six species, including the

Glittering-throated Emerald, have been allocated the genus *Polyerata*. They are unified by a dark upper mandible, a pale ventral region and lack of rufous in the tail. The Andean Emerald belongs in a third genus, *Agyrtia*, comprising nine species with largely white underparts, including the throat. The final nine species have adopted the genus *Saucerottia* characterized by their glossy violet or purplish tails, as illustrated by this Steely-vented Hummingbird.

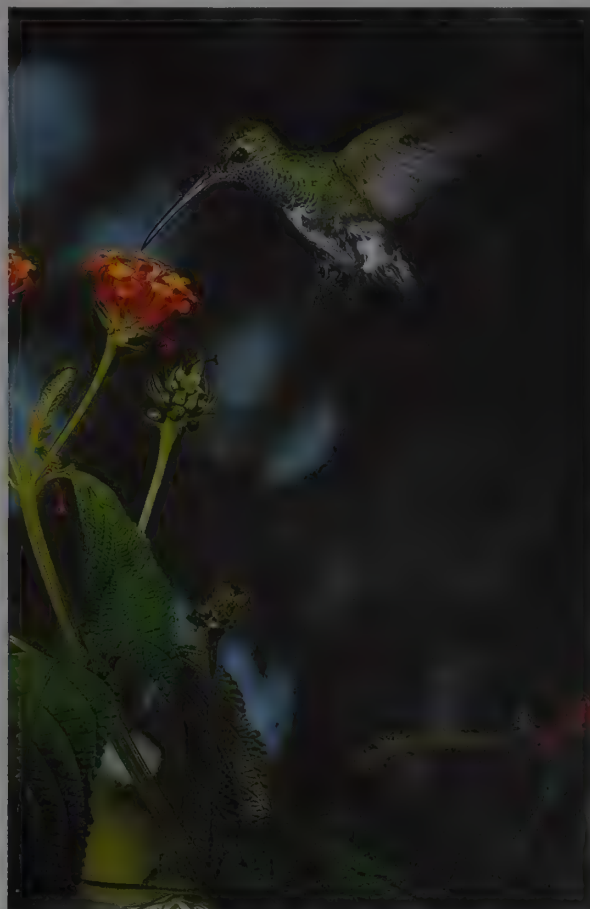
[Above left: *Amazilia tzacatl fuscicaudata*, Antioquia, Colombia.

Above right: *Polyerata fimbriata apicalis*, Meta, Colombia.

Below left: *Agyrtia franciae franciae*, Tolima, Colombia.

Below right: *Saucerottia saucerrottei saucerrottei*, Valle, Colombia.

Photos: Luis Mazariegos]





Of 23 hummingbirds described to science between 1946 and 1995, only five are still considered valid. The rest have been relegated to the ranks of races, hybrids or aberrant forms. In some cases, however, studies have led to the splitting of previously recognized species. The genus *Aglaiocercus*, for example, was formerly treated as monospecific but is now considered to contain three species, one of which is the Violet-tailed Sylph. While the three are very similar, they differ in plumage coloration, notably in the underparts of females, as well as in size and altitudinal range.

[*Aglaiocercus coelestis* *coelestis*, La Planada Reserve, Nariño, Colombia. Photo: Patricio Robles Gil/Sierra Madre]

muscle (*Musculus splenius capitis*), place the "tooth-bills" *Androdon* and *Doryfera* at the base of the trochiline assemblage, followed by a more derived taxon containing the "sabrewing-and-mango" genera *Campylopterus* (including *Phaeochroa*, *Eupetomena*, *Aphantochroa*), *Florisuga* (including *Melanotrochilus*), *Colibri*, *Anthracothorax* (including *Avocettula*), *Topaza*, *Eulampis*, *Chrysolampis*, *Orthorhyncus*, *Klais*, *Stephanoxis*, and *Abeillia*. This assemblage is characterized by complex cervical musculature, similar patterns of song syntax, and small compact nests of little variation in form and structure, often placed on leaves or saddled on horizontal branches. Probably closely related to the "sabrewing-and-mango" genera are the "coquettes" *Lophornis* and *Discosura* (including *Popelairia*), based on nest shape and male frontal display patterns.

The next taxon comprises the "true emeralds" *Trochilus* and *Chlorostilbon* (including *Chlorestes*). Biogeographical history and plumage features in both males and females already suggested close affinities between members of the West Indian taxa of *Trochilus* and *Chlorostilbon*, an assumption supported by a typical song pattern exhibited during the male display, and also by similarities of nest structure and site. Based on the colour patterns of the rectrices and other morphological features, their closest relatives are most likely the "emeralds" *Panterpe*, *Elvira*, *Eupherusa*, *Goethalsia* and *Goldmania*, followed by the "woodnymph-and-sapphire" clade *Cynanthus*, *Thalurania*, *Damophila*, *Lepidopyga*, *Hylocharis* and *Chrysura*. This latter assemblage shows distinctive cervical musculature, unique flight patterns in the male display, and nest structures with close affinities to the emeraldines. Another unit consists of the "amaziline emeralds" *Leucochloris*, *Polytmus*, *Leucippus*, *Amazilia*, *Agyrtria*, *Polyerata* and *Saucerottia*. Typical nest forms, nest-sites, and a cervical musculature pattern characterize this clade. A recent biogeographical revision of the taxa formerly treated superficially under the genus *Amazilia* postulated a polyphyletic status and various centres of origin around the periphery of central South America. Plumage character analysis suggests ties to *Lepidopyga* and *Leucippus*.

Another distinct taxon also derived from plumage comparisons are the "mountain gems" *Microchera*, *Anthocephala*, *Lampornis*, *Basiliinna* (formerly treated under *Hylocharis*) and *Lamprolaima*.

The "brilliant" *Clytolaema*, *Heliodoxa* (including *Polyplanta*), *Hylonympha* and *Sternoclyta* comprise a further assemblage of closely related taxa. This group is united by typical morphological features like feathered upper and lower mandibles, throat coloration, song and display patterns.

The large "Andean clade" consists of five sub-units: the first contains *Urochroa*, *Boissonneaua* and *Aglaeactis*; the second *Oreotrochilus*, *Lafresnaya*, *Coeligena*, *Ensifera*, *Pterophanes*, *Patagona* and *Sephanoides*; the third *Helianthus*, *Eriocnemis*, *Haplophadna*, *Urochroa* and *Ocreatus*; the fourth *Lesbia*, *Sappho*, *Polyonymus* and *Ramphomicron*; and the fifth *Oreonympha*, *Oxygogon*, *Metallura*, *Chalcostigma*, *Opisthoprora*, *Taphrotesbia* and *Aglaiocercus*. This arrangement is based on the following common features: open wing presentations after perching (especially members of the first, second and third groups); distress calls; perching displays; advertisement songs; plumage characteristics; nest shape; and nest-site.

Finally, another distinct assemblage, the "starthroat-and-woodstar" group, containing *Heliothraupis*, *Rhodopis*, *Thaumatococcus*, *Tilmatura*, *Doricha*, *Calliphlox* (including *Philodice*), *Microstilbon*, *Calothorax*, *Mellisuga*, *Archilochus*, *Calypte*, *Atthis*, *Stellula*, *Myrtis*, *Myrmia*, *Chaetocercus* (including *Acestrura*) and *Selasphorus*. Some of these share similarities in plumage characteristics, notably an eclipse plumage; display pattern features; song structure; flight displays; nest shape; and nest-site.

It should be noted that some of the aforementioned genera are so closely related that their separate generic status is doubtful. The systematic treatment of several other trochiline genera, such as *Heliactin* and *Loddigesia*, is problematic due to lack of data on their anatomy and behaviour. Nest characteristics of *Heliothryx*, another genus with uncertain ties, indicate affinities to the more primitive trochilines like *Colibri* and *Anthracothorax* as well as to *Heliactin*. Another taxon with unresolved phylogenetic relationships is the Central and North American monotypic genus *Eugenes*. Behaviourally, the Magnificent Hummingbird (*Eugenes fulgens*) shows close affinities to the Central and South American genus *Heliodoxa*, but its cervical musculature indicates ties to the North American genus *Archilochus*.

The arrangement of trochiline clades based on comparisons of display patterns, song structure, nest shape, and morphological features should be considered as provisional. Although these

Improved knowledge of the life history of the Black-billed Streamertail of Jamaica has resulted in its formal separation from the Red-billed Streamertail (*Trochilus polytmus*), with which it was considered conspecific. They are closely related and largely allopatric, but in the small area of overlap in the western John Crow Mountains interbreeding takes place only rarely. Even though this decision results in both members of the genus being endemic to one island, they are unlikely to be threatened because they readily tolerate man-modified habitats such as banana plantations and gardens.

[*Trochilus scitulus*,
Port Antonio, Jamaica.
Photo: Robert Tyrrell]



data sets are extremely helpful for the reconstruction of trochiline phylogeny, many of the characters are known only for some taxa but missing for others. Therefore the taxa proposed may stand or fall with further data analyses of homologous characters, a major problem in the evaluation of structure, function or behaviour.

Most promising for a phylogenetic reconstruction of the trochilines seems to be the study of nest structure and nest-site. For each of the eleven trochiline taxa hypothesized, nests show typical patterns within each assemblage. Perhaps the hummingbird family is, like the tyrant-flycatchers, a group for which nest data may be a highly effective tool in reaching an accurate classification. Unfortunately, for several key taxa no nest descriptions exist.

If these preliminary taxonomic divisions, derived mainly from morphology and behaviour, are compared with recent allozyme and DNA hybridization studies (on less than 10% of all hummingbird species), only a few phylogenetic congruencies can be stated with any certainty. The latest molecular data confirm the division of the two basic subfamily lineages, the hermits and the typical hummingbirds (trochilines). Within the trochiline lineage, the relative positions of genera like *Androdon*, *Doryfera*, *Colibri* and *Eulampis* were confirmed, while *Lesbia*, *Coeligena*, *Oreotrochilus* and *Agelaiocercus* appeared as members of the same Andean cluster as that proposed by non-molecular studies. Different to the traditional classification are the relationships of *Chlorostilbon*, *Campylopterus*, *Orthorhyncus*, *Amazilia* and *Thalurania*, as well as that between the Andean assemblage and *Discosura*. Most taxonomists are sceptical of these new findings, particularly since broad generalizations within and between genera are made. Frequently only one species of a genus has been analysed in these studies, with risky extrapolations as to the systematic status of the taxon under consideration, ignoring possible polyphyletic relationships within the genus. It is notable that some results of these molecular biology studies, using similar methods, have led to different branchings for the same trochiline group. Without a representative study of a larger number of replicates covering a larger diversity of hummingbird taxa, formal taxonomic changes based on molecular biology methods should be considered only with caution.

Using plumage characters, there is little disagreement as to which forms of hummingbird should be treated as species. However, problematic specimens or even taxa exist, mostly among trochilines found in museum collections. Some of these enigmatic hummingbirds may be diagnosed as atavistic specimens, hybrids or melanistic morphs of distinct species. An interesting example of the confusion that can be caused is provided by the

Pale-tailed Barbthroat (*Threnetes niger*), which was previously known as *T. leucurus* until it was discovered that the form hitherto listed as *T. niger* was merely a melanistic morph of the same species, with the result that the older name, *niger*, had to replace *leucurus*, since it has priority. The scientific literature refers to dozens of obscure taxa, generally listed as intergeneric hybrids. This high frequency of hybrids between taxa of two genera is often interpreted as evidence that genera are oversplit. However, based on the lack of intrageneric hybrids among North American trochilids it has been assumed that the perfection of intrageneric isolating mechanisms without the concurrent development of intergeneric isolating mechanisms is a major cause of evolutionary change.

It is notable that the North American trochilids of the genera *Archilochus*, *Calypte*, *Stellula* and *Selasphorus*, which regularly hybridize across their generic boundaries, belong to very closely related species within the "starthroat-and-woodstar" lineage. However, hybrids between distinct genera like *Eugenes* x *Cynanthus*, *Heliodoxa* x *Heliangelus*, and *Agelaiocercus* x *Thalurania* have been identified. Recently it has also been shown for the Phaethornithinae that regular intrageneric hybridization occurs, but due to plumage similarities among parent birds parentage can only be determined by means of detailed biogeographical and morphometric information. With a better knowledge of hummingbird phylogeny, hybridization at different taxonomic levels may contribute to our understanding of generic relationships.

Biogeographical studies combined with morphological parameters may reveal more cases of hybridization, especially when only single specimens of a taxon are known, as in the eastern Venezuelan "Amazilia distans", now considered a hybrid between race *elegantissima* of the Glittering-throated Emerald (*Polyerata fimbriata*) and race *viridiventris* of the White-chinned Sapphire (*Hylocharis cyanus*).

During the period 1946-1995, altogether 23 hummingbird species new to science were described, with eight in Phaethornithinae and 15 in Trochilinae. After critical revision only one of the hermits, Koepcke's Hermit (*Phaethornis koepckeae*), was considered a valid species, while only four remained on the list of trochilines, namely the Royal Sunangel (*Heliangelus regalis*),

Because of considerable morphological differences, the Ecuadorian Hillstar has been split from its relative, the Andean Hillstar (*Oreotrochilus estella*), to form a pair of allospecies. They inhabit the windswept páramo at high altitudes, where the bulk of their diet is derived from the flowers of composite shrubs, on which they often prominently perch, as illustrated by this female. Like most hummingbirds, they are largely solitary but considerable aggregations sometimes gather at superabundant nectar sources. In addition, both species sometimes roost and nest semi-colonially in caves, presumably for shelter in their open montane environment.

[*Oreotrochilus chimborazo jamesonii*,
Papallacta Pass, Ecuador.
Photo: Luis Mazariegos]





Colorful Puffleg (*Eriocnemis mirabilis*), and Perija (*Metallura iracunda*) and Neblina Metaltails (*Metallura odomae*). The others turned out to be subspecies, hybrids, aberrant individuals, immatures, or synonyms of known subspecies.

The Chiribiquete Emerald (*Chlorostilbon olivaresi*), described in 1996 by F. G. Stiles, is presently considered a valid species but



may in the future end up being treated only as a subspecies of the Blue-tailed Emerald (*Chlorostilbon mellisugus*), once more detailed information on geographical character variations are available and zones of contact within this complex are better understood.

It is highly likely that some new hummingbird species will be discovered in forthcoming years, since many areas, especially in the Andes and isolated Andean foothills, are still ornithologically unexplored. Further life-history knowledge may also reveal that some of the known taxa, currently treated as subspecies, have successfully developed reproductive isolating mechanisms, thus calling for their recognition as full species, as was quite recently the case of the Red-billed (*Trochilus polytmus*) and Black-billed Streamertails (*Trochilus scitulus*).

Besides these general speciation problems for taxonomists, more basic taxon-related questions in hummingbirds still remain unanswered. Females are unknown for several taxa, such as the Coppery Thorntail (*Discosura leucophaea*) and the Sapphire-bellied Hummingbird (*Lepidopygia lilliae*). Some taxa such as the Turquoise-throated Puffleg (*Eriocnemis godini*), Black-backed Thornbill (*Ramphomicron dorsale*) and several others have not been sighted for decades. They may have survived in remote and inaccessible places or may be extinct, as seems to be the case with the possibly hybrid Bogota Sunangel (*Heliangelus zusii*) from the eastern Colombian Andes, and also with Brace's Emerald (*Chlorostilbon bracei*) from New Providence, Bahamas, not seen again after its discovery in 1877 (see Status and Conservation). The very absence of recent records and material for such forms makes it extremely difficult for any advances to be made regarding their taxonomy, as is certainly the case of the possible species "*Saucerottia alfaroana*", of which there are no recent records, and which may be extinct. Differing opinions consider this form to be a genuine species, or to belong either in the Indigo-capped Hummingbird (*Saucerottia cyanifrons*) or in the Steely-vented Hummingbird (*Saucerottia saucerrottei*), but the chances of its being an aberrant individual or of hybrid origin equally remain open.

Morphological Aspects

Hummingbirds are extremely small. Most species are 6-12 cm in size and have a body mass of around 2.5-6.5 g. The Reddish

The taxonomy of the Variable Mountain-gem is highly controversial. Herein it is treated as a composite of three parapatric groups that are sometimes recognized as full species: the purple-throated, blue-tailed calolaemus group; the white-throated, grey-tailed form cinereicauda; and the white-throated, blue-tailed form castaneoventris. Females of all three are virtually identical, while hybrid zones occur in areas where their ranges meet. Research has shown the sexes to be ecologically separated, feeding on nectar at different vegetational strata, the female tending to feed much lower down.

[*Lampornis castaneoventris*, Costa Rica. Photo: Michael Fogden/Oxford Scientific Films]

Small size is a famous feature of most hummingbirds, but the diminutive Bee Hummingbird takes smallness to extremes. Weighing about 2 g, the male is the lightest bird in the world, easily mistaken for an insect as it whirrs slowly around the blossom of Aloe and Hibiscus in its native Cuba. The male's glittering red gorget and lateral plumes distinguish him from the dull plumaged but slightly larger female.

[*Mellisuga helenae*, Playa Larga, Zapata Swamp, Cuba. Photo: Robert Tyrrell]

Hummingbirds have perfected the art of hovering in order to exploit the rich nectar resource of flowering plants in the New World.

The birds can remain apparently motionless in mid-air for quite some time, their wingtips executing rapid figures-of-eight, as partly captured on this Green-backed Firecrown. During foraging flight, 10-80 wingbeats per second are the norm, although up to 200 beats per second have been recorded during displays.

Unlike other birds, the Trochilidae use both the upstroke and the downstroke to power their flight.

[*Sephanoides sephaniodes*, southern Chile.

Photo: Günter Ziesler]



Hermit (*Phaethornis ruber*) from Guyana and Brazil and the Bee Hummingbird (*Mellisuga helenae*) of Cuba each weigh less than 2 g (1.6-1.9 g), while members of the genera *Eutoxeres*, *Ensifera* and *Pterophanes* are heavier than average at 12-14 g. As its name suggests, the largest of all is the Giant Hummingbird (*Patagona gigas*), weighing 19-21 g, comparable in size to a swift.

Trochilids are highly evolved nectarivores, depending almost completely on the carbohydrate-rich sugar secretions (nectar) of ornithophilous flowering plants, the approximate composition of their diet being 90% nectar, and 10% arthropods and pollen. They reach this liquid food with thin, elongated bills of various shapes, which protect their specialized long, sensitive tongues. Their feeding behaviour necessitates a specific locomotor performance,

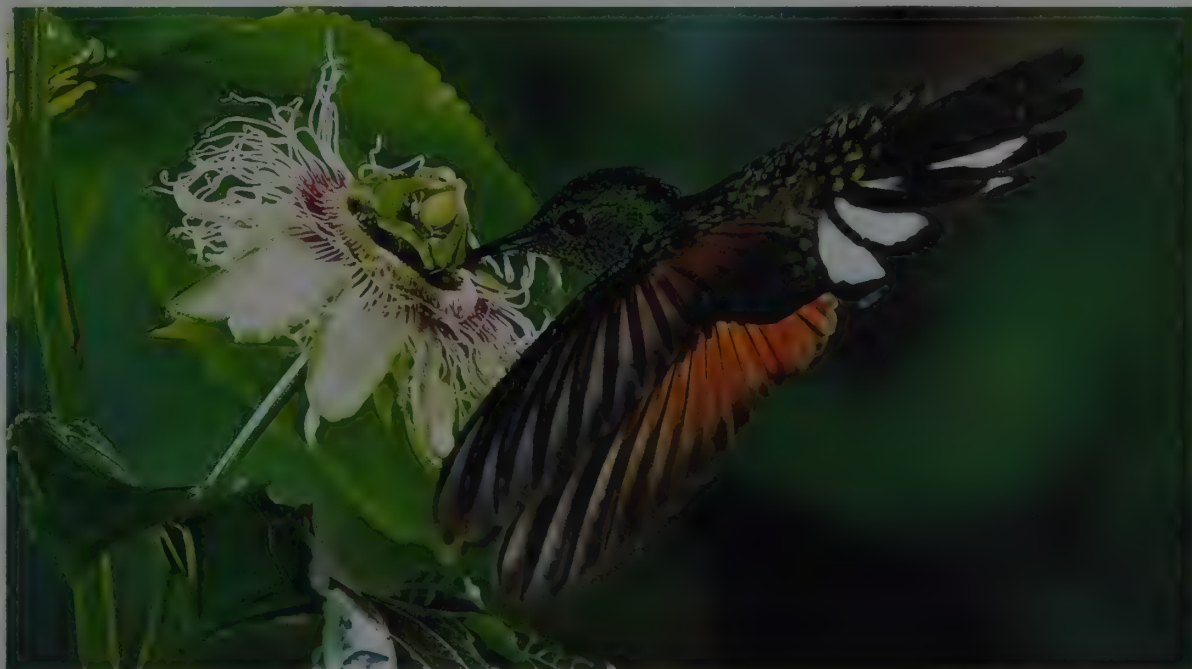
namely hovering flight, which allows them to remain apparently motionless in the air when feeding on exposed flowers, but, due to this unique foraging behaviour, they can no longer walk or climb with their feet, which serve only for perching. During hovering, their pointed, uncambered wings are moved mainly in the horizontal plane, describing with their tips a flat figure of eight, in the manner of a variable-pitch rotor. By slightly altering the wing angle, this technique allows all kinds of controlled forward, sideward and backward movements in the air, including upside-down manoeuvres.

While hovering, the wingbeat rate in smaller trochilids like the Amethyst Woodstar (*Calliphlox amethystina*) averages 70-80 per second compared to 10-15 in the Giant Hummingbird.

Supremely manoeuvrable, all hummingbirds can control their position and orientation with minute adjustments in the angle or strength of their wing strokes, often performing acrobatics to access hidden nectar reserves.

The Stripe-tailed Hummingbird, here demonstrating its flying skills at a passionflower (*Passiflora*), is found mainly in moist montane forest in Central America, where it feeds at flowering trees, epiphytes and shrubs.

[*Eupherusa eximia egregia*, Costa Rica. Michael Fogden/DRK]





The hermit subfamily, Phaethornithinae, is separated from the typical hummingbirds of the Trochilinae, its members differing chiefly in their unique humeral tendon, their dull colours and their distinctive habit of constantly tail-wagging when perched. The vast majority of hermit species inhabit the forest understorey, where they are non-territorial and display at leks, features only shared by a few trochilines. In their displays, male hermits usually form loose aggregations, fan their rectrices and call with wide open bills revealing their brightly coloured gapes. The Green Hermit, like most of its relatives, has developed a long bill adapted for insertion into flowers with elongated corollas. The hovering flight of both hermits and trochilines is facilitated by skeletal design. While most birds have six pairs of ribs, hummingbirds possess eight, along with a deeply keeled, elongated sternum to which powerful flight muscles are attached. The sternum has a shallow cup-and-ball joint where the strong coracoid bones are connected, a design shared only by the swifts. The "arm-bones" of hummingbirds are truncated while the "hand-bones" carry ten large primaries, increasing steadily in size towards the outer edge of the wing. The number of secondaries is much reduced, there being six or sometimes seven, compared with the usual nine of most passerines.

[*Phaethornis guy emiliae*,
Valle, Colombia.
Photo: Luis Mazariegos]

The feet of the Black-crested Coquette have been reduced to very weak appendages that are useless for hopping, walking or climbing.

This is true of all hummingbirds because of their reliance on hovering and the constraints imposed by associated flight dynamics. In addition, hummingbirds and swifts possess complex cervical musculature, the function of which is unclear. It may relate to the control and speed of head movements, which are important for trapping mobile insect prey, but as insects only make up a rather small part of the diet of hummingbirds, there might be other benefits for aerial nectarivores.

[*Lophornis helenae*,
Costa Rica.

Photo: Michael Fogden/
Bruce Coleman]



During the courtship flights of some North American trochilids, such as the Ruby-throated Hummingbird (*Archilochus colubris*) and the Rufous Hummingbird (*Selasphorus rufus*) wingbeat rates of over 200 per second have been reported. The humming sound produced by the wings during hovering has given the family its English name.

Flying speeds under controlled laboratory conditions range roughly from 48 to 85 km per hour. For the Green Violet-ear (*Colibri thalassinus*), in the wild, a velocity of 96 km per hour has been recorded, and during short chase flights up to 150 km per hour. The homing pigeon, a domesticated form of the Rock Dove (*Columba livia*), and one of the most skilful and rapid fliers among birds, travels at speeds of around 64 km per hour.

The unique flight mode involves specific skeletal and flight-muscle features. The deeply keeled and elongated hummingbird sternum is relatively large compared with those of other flying birds. Eight pairs of ribs, two more than in most birds, help to stabilize the body during flight. Exceptional in structure are the strong coracoids of the pectoral girdle. Only hummingbirds and swifts have a shallow cup-and-ball joint where the coracoids are connected to the sternum. Tendons connect the flight muscles with the humerus.

The arm bones of all trochilids, consisting of the humerus, radius and ulna, are much shortened, with the result that over 70% of the wing skeleton size is attributable to the elongated hand bones, homologous to the second, third and fourth fingers of the tetrapod hand.

The modified humerus bone of hummingbirds moves freely at the shoulder joint, permitting optimal wing movement in all directions, including axial rotations of nearly 180 degrees. It is only the humerus that moves at this joint. Slow motion pictures, however, indicate little flexure of the short arm bones.

The hand bones bear 10 large flight-feathers, the primaries, increasing progressively in size from the inner portion of the wing towards the tip. There are only a few exceptions to this general size scheme, such as in the Broad-tailed Hummingbird (*Selasphorus platycercus*) and the two Jamaican *Trochilus* streamertails, with their somewhat reduced outer primaries. In the case of the Broad-tailed Hummingbird these form modified thin wingtips creating a specific mechanical flight sound. In the streamertails, the sound source sometimes attributed to the reduced outermost primaries is still debated, but most likely this mechanical flight noise is generated by the scalloped and fluted pair of elongated tail feathers. Another unusual group of

trochilines, with up to three modified outermost primaries, is the sabrewing assemblage (*Campylopterus*). Their feather shafts are thickened to various degrees, mainly in males, possibly contributing to a strengthening of the wing during their fast, swift-like gliding among semi-open vegetation, a common feature of these hummingbirds.

The two major muscles for trochilid flight are the mitochondria-rich *Musculus pectoralis major*, attached to the sternum, clavicle and humerus, and the *Musculus supracoracoideus*, lying beneath the pectoralis and also attached to the sternum. Both muscles consist exclusively of dark red fibres, providing the en-

In spite of their feet being tiny, hummingbirds use perches frequently, particularly when suitable sites are provided by favoured food plants, such as *Heliconia*.

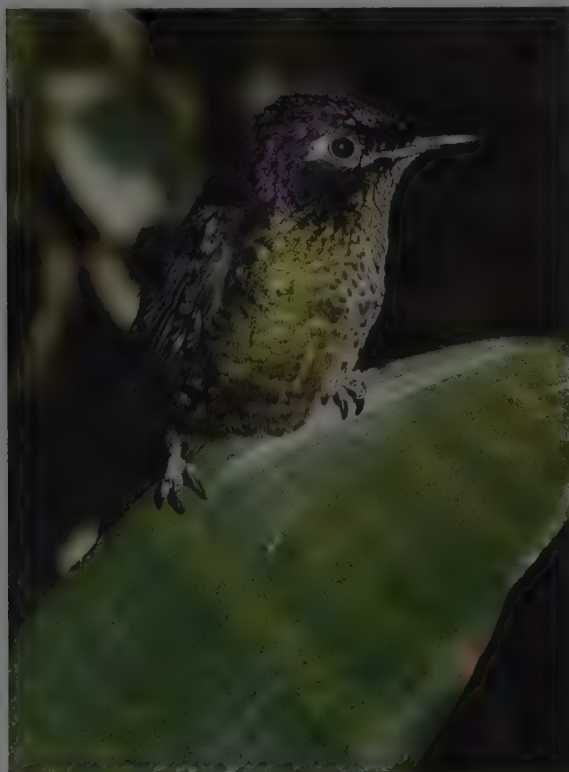
The distinctive Buff-tailed Sicklebill is celebrated for its startling bill morphology, a design that allows it to harvest the nectar of similarly curved *Heliconia* and *Centropogon* flowers.

This species is not exclusively reliant on humid forest, also occurring in open habitats and areas that are cultivated or disturbed.

[*Eutoxeres condamini*
condamini,
Serranía de los
Churumbelos, Cauca,
Colombia.

Photo: Luis Mazariegos]





ergy for powerful flight. The large pectoralis pulls the wing down, whereas the antagonistic supracoracoideus raises it. Since wing movement during hovering is extremely energy-demanding the supracoracoideus is also large, amounting to about 50% of the size of the pectoralis. Thus hummingbirds use the upstroke and downstroke almost equally for powered flight, in contrast to most other birds which mainly employ the downstroke for their powered flight. Both flight muscles together make up over 30% of the body mass of a hummingbird, much more than in other strong fliers such as migratory birds, in which these muscles account for about 20% of body mass.

As tiny endotherms, hummingbirds suffer from low thermal inertia and high heat loss. Flapping flight is energetically expensive, and convective cooling caused by wing and air movements can further exacerbate energy loss. Energy conservation during flight is thus an important physiological problem for hummingbirds. Studies by P. Chai and his co-workers revealed that trochilids clearly use the heat produced in flight to contribute to their thermoregulatory requirements during hovering. If oxygen consumption is used as an estimate of metabolic cost, it was demonstrated that in hover-feeding, oxygen consumption increased only moderately between 5°C and 35°C, in contrast to the drastic increase during perch-feeding by hummingbirds over the same temperature range. Heat production by contraction of the flight muscles is employed as a substitute for regulatory thermogenesis to compensate for heat loss during exposure to cold. The mechanical power requirements of hovering decrease slightly with declining air temperatures, but metabolic costs increase. Thus the mechanical efficiency of muscles in converting metabolic power into mechanical power is reduced. Changes in wingbeat kinematics also accompany this reduction in muscle efficiency. Wingbeat frequency increases but stroke amplitude decreases when hovering at low temperatures, indicating a thermoregulatory role for the flight muscles. It has been suggested that a modulating of muscle efficiency and heat production may allow flying hummingbirds to achieve energy conservation during cold conditions.

Hummingbird flight muscles are extremely oxygen-dependent. Mitochondrial volume density in these muscles can account for 35% of their volume; this figure may represent an upper limit because any further increase would reduce space for the muscle fibre necessary for mechanical work. However, even during hov-

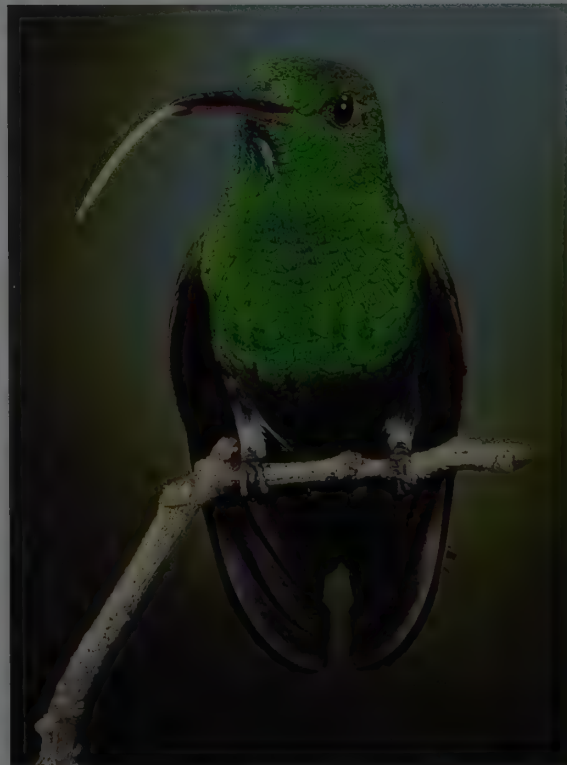
ering, trochilids are operating within a reasonable physiological safety margin. These physiological reserves are essential for maintaining fitness parameters. A steep decline in hover-feeding duration with decreasing oxygen density has been observed in the laboratory for the Sparkling Violet-ear (*Colibri coruscans*) of South America. This fairly large montane species was capable of hovering at simulated altitudes of over 6000 m with only a slight increase in oxygen consumption of 6-8%. Recently it has been discovered that this increase at low air densities (high altitudes) matched the required increase in flight power output, resulting in a constant muscle efficiency of 10-11%, assuming perfect elastic energy storage.

Another specialized trochilid muscle is the heart. It amounts to about 2.5% of a hummingbird's body mass, whereas in small songbirds, like the House Sparrow (*Passer domesticus*), it contributes 1.3% of the weight, and only 0.5% in primates. A hummingbird's heart beats 500-600 times per minute while the bird is resting, and over 1000 times per minute during aggressive encounters. In a ratite like the Ostrich (*Struthio camelus*) the normal heart rate ranges around 40-180 beats per minute.

The peculiar crossover origin of the cervical *Musculus splenius capitis*, attached to the second vertebra, is a complex myological feature found in hummingbirds and swifts (see Systematics). The function of this muscle has been a matter of speculation since the discovery of its cruciform emergence by P. J. K. Burton in 1971. In hummingbirds and swifts it is most likely that this muscle type ensures faster sideways head movements than can be made by species with a *Musculus splenius capitis* attachment to the neural spine, as in passerines for example, where the shorter fibres of this muscle imply relatively slower head movements; in these taxa, the central emergence of this muscle mainly supports up-and-down movements of the head. Hummingbirds and swifts feed on insects at high flight velocities. Since they can recognize their prey only at short distances, high-speed head movements are required to select and capture suitable food.

All contour feathers of trochilids are connected to cutaneous muscles which co-ordinate feather movements like fluffing or ruffling for thermoregulation and comfort behaviour, as well as the expansion of iridescent gorgets or rectrices as specific recognition signals during territorial defence or flight display.

The reduced wing bones of trochilids normally carry six, occasionally seven, short inner flight-feathers, the secondaries.



One of the shortest bills of any hummingbird is that of the Purple-backed Thornbill. It is used to obtain nectar from a wide variety of small-flowered shrubs and even large flowers, utilizing holes at their bases made by *Diglossa flowerpiercers*. It is also used for capturing insects. The energy required to fuel the intense muscular activity of hovering flight is derived from carbohydrates in nectar. A hummingbird's heart accounts for about 2.5% of its mass, around double the normal proportion for birds and five times that of primates. To meet the high oxygen needs of their lifestyle, it beats 500-600 times per minute when the bird is perched.

[*Ramphomicron microrhynchum*.
Photo: A. J. Mobbs/Aquila]

Hummingbirds consume nectar with the use of an extendable bifurcated tongue. While the base is partly cartilaginous, the tip is divided lengthwise to form two separate membranous curled troughs. Nectar passes into these grooves by way of capillary action and the tongue is flicked 3-13 times per second. The function of the mandibles in the nectar-drinking process remains unclear, although it appears that they might be pressed together to squeeze nectar from the tongue. Equally, the tongue might be stretched slightly, as by this Berylline Hummingbird, to constrict the capillaries and thus flush nectar into the throat.

[*Saucerottia beryllina*
viola,
La Petaca, Sinaloa,
Mexico.
Photo: Robert Tyrrell]

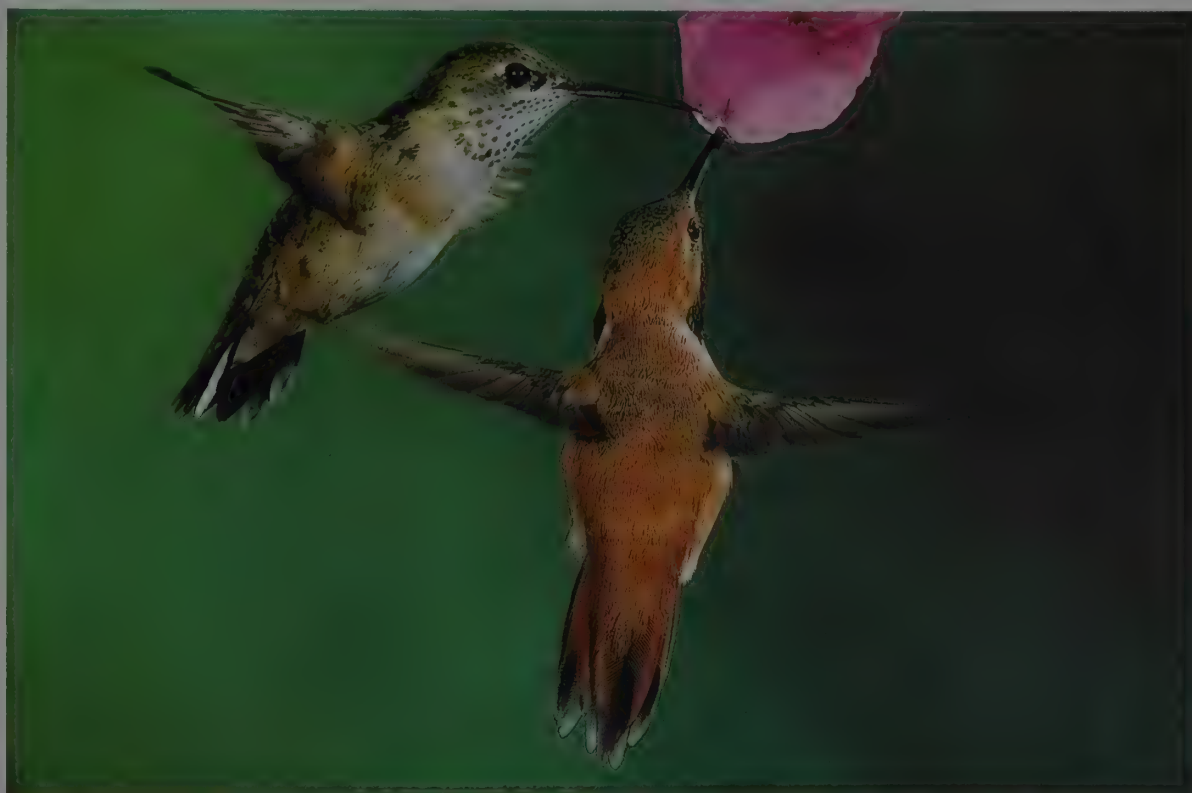
Most trochiline species, such as these Rufous Hummingbirds, are sexually dimorphic, males usually being considerably brighter than females.

Energy conservation presents an important physiological problem to flying hummingbirds, especially at the high latitudes where this species breeds.

When temperatures are low, the contraction of flight muscles assists with thermoregulation by compensating for heat loss. Individuals also tend to increase their rate of wingbeats but decrease the amplitude of each beat, thus increasing heat production while maintaining controlled flight.

[*Selasphorus rufus*,
Rocky Mountains,
Montana, USA.

Photo: Kenneth Fink]



Differences of flight specialization in birds result in a variable number of secondaries, whereas the number of ten primaries remains fairly constant, except for grebes (Podicipedidae), storks (Ciconiidae) and flamingos (Phoenicopteridae) with eleven primaries and the New World nine-primaried songbirds, like tanagers (Thraupidae), wood-warblers (Parulidae) and buntings (Emberizidae). A soaring flight specialist like the Wandering Albatross (*Diomedea exulans*) has ten primaries but 37 secondaries, while most passerines have only nine secondaries.

The number of tail feathers or rectrices in hummingbirds is almost invariably 10, except for the Marvellous Spatuletail (*Loddigesia mirabilis*) of Peru which has only four. In adult males of this species, one pair is highly modified with a forward-curved quill ending in a fairly large racket. Tail feathers play an important role in all flight manoeuvres. They are essential for lift and balance during quick flight movements in dense forest undergrowth, and for progressive or abrupt changes from fast forward to hovering flight.

Hummingbirds' tails differ greatly in size and shape. They can be forked, V-shaped, rounded or wedge-shaped. In several species of the genera *Lesbia*, *Trochilus* and *Thaumastura*, for example, some of the tail feathers are strikingly elongated, the same length or even twice as long as the actual body size of the bird. Others, like the Racquet-tailed Coquette (*Discosura longicauda*) and Booted Racquet-tail (*Ocreatus underwoodii*), carry little flags at the end of a single pair of extended rectrices.

Unlike their rectrices, hummingbirds' wings often appear rather dull since the colour of the remiges is pigment-based, as in almost all other birds. Exceptions are the brightly shining wing-coverts of many species and the iridescent flight-feathers of the Purple-throated Carib (*Eulampis jugularis*). The lack of iridescent colours in primaries and secondaries is obviously an adaptation for flight, since a characteristic anatomical feature of feathers producing structural colours is the absence of hooklets between the barbules, reducing the mechanical strength of the feather vane.

Another major feature of trochilid plumage is the striking iridescent colours of crests, gorgets, rectrices and other feather structures. In contrast to colours generated by pigments, iridescence is of a physical nature, caused by the structure of platelets in the feather barbules. Beneath the upper surface of these platelets we find thin elliptical bodies of melanin filled with air bub-

bles. These form a mosaic-like non-homogenous layer of up to ten, stacked one above the other within a barbule. The platelets are only 2.5 microns in length with a thickness averaging 0.18 microns. The melanin matrix of the platelets has a refractive index of 2.2, the air bubbles inside of 1.0. With varying air volume in the platelets, different composite refractive indices are created, ranging from 1.85 at the red end of the spectrum to 1.5 at the blue end. C. Greenewalt discovered by electron microscopy that the thickness of the platelets influences not only the properties of the perceived light, but also those of the air held inside each pigmented body, thus causing variations in interference effects. Each pigmented body within a platelet can produce differ-



Hummingbirds' tails differ greatly in size and shape, but they generally function in flight control and manoeuvrability. In particular, they assist with lift and provide balance during adjustments between direct and hovering flight.

The tails of several species, such as the Empress Brilliant, are deeply forked, which maximizes flight control while minimizing drag.

This highly iridescent species has a restricted range in western Colombia and Ecuador, where it is locally common in the forests of wet foothills and lower mountains.

[*Heliodoxa imperatrix*,
Río Nambi Reserve,
Nariño, Colombia.

Photo: Luis Mazariegos]



ent colours depending on the angle from which it is viewed. Thus, a throat may appear metallic golden if a beam of light comes from directly behind the observer, but will shift to almost black if the angle of view is changed. In summary, media of two different structures are necessary to produce interference. In hummingbirds these are mainly the upper surface of the barbules and the air-containing cells of the platelets. When light waves are reflected from such a bi-medium structure so that the crest of one wave coincides with the trough of another of the same wavelength, then they neutralize each other. Other wavelengths then effectively stimulate colour vision.

Hummingbird coloration is related to behaviour. Generally two broad groups of coloration characteristics can be distinguished in birds: those promoting concealment and those enhancing conspicuousness. The majority of trochilid females exhibit a cryptic coloration. This may be viewed in the light of predator-prey relationships, since all activities associated with nesting and the rearing of the young are carried out by the female alone. Conspicuous female coloration would easily betray the bird and the nesting site to potential predators. Males of many species of open habitats often show phaneric coloration, which makes them stand out as much as possible. As part of their territorial and polygamous life-history, bright, light-dependent iridescent colours on the throat, crest or back play important intraspecific and interspecific roles as visual threat signals for territorial defence, self-advertisement during display, or species-specific recognition cues. Since colour signals are effective only at close range, hummingbird visual behaviour is often accompanied by a complex vocal repertoire and/or mechanically produced sounds. In forest-dwelling species, like most members of the Phaethornithinae, sex-specific phaneric iridescent coloration is absent. This may be explained by the dimly lit undergrowth of their tropical forest habitats and by their non-territorial foraging behaviour.

Hummingbirds lack downy feathers when adult. Some sparse natal down occurs in a few longitudinal rows on the upperparts of nestlings. These neossopiles, normally light beige or dull greyish in colour, remain attached to the contour feathers during the nestling stage, where they serve as triggers to release gaping (see Breeding). They are shed some weeks after fledging.

Trochilids have proportionally few contour feathers, roughly in the range of 900-1700, about 4-7 times less than passerines of similar size. This is considered to be an adaptation to high heat production during flight. Heat dissipation is much easier to regulate with less feather insulation.

The plumage of immature males and females is mainly similar to, but duller than, that of adult females. Immatures moult into adult plumage in their first year. In only a few sexually dimorphic species, like the Jamaican streamertails and the Juan Fernandez Firecrown (*Sephanoides fernandensis*), male and female nestlings can already be clearly separated by their plumage, which is similar to that of adults but less bright in coloration.

Hummingbirds have a single complete annual moult, starting soon after the breeding season. Replacement is slow and takes several months: post-juvenile moult takes around four months, annual moult about 4-5 months. The post-juvenile moult is lacking in the Western Long-tailed Hermit (*Phaethornis longirostris*) of Central America, formerly considered as conspecific with the Eastern Long-tailed Hermit (*Phaethornis superciliosus*), and it may also be absent in other lekking tropical species. In general, the flight-feather moult of hummingbirds resembles that of most other avian taxa. Primaries are replaced in descendant sequence, starting from the innermost and moving to the outermost. However, only trochilids invert the moult of the outermost two primaries (P1-P8, P10, P9), which are crucial in maintaining aerodynamic stability of the wingtip during hovering flight. Moult of secondaries follows in a centripetal order, and with a high degree of individual variation following the replacement of the majority of the primaries. This is also a common moult pattern in most birds to avoid creating gaps in the flight surface. The renewal of the rectrices, usually replaced from the centre outwards, is different in trochilids. The outer rectrix is normally moulted earlier in the sequence rather than last. Bilateral asymmetry of the replacement of rectrices and secondaries is common. Body moult is initiated with the shedding of the primaries and continues until their replacement is completed, though with much individual variation. In several hummingbird species the wing-coverts and tail-coverts are moulted simultaneously with the replacement of primaries, but their moult is complete before that of the flight-feathers. Moult of iridescent feather parts on the throat, chin, forehead and crown of males is often completed several weeks after renewal of primaries. It has been suggested that the delayed moult of brightly coloured feathers ensures that the bird enters the subsequent breeding season in optimal plumage condition.

An interesting moult pattern has been observed in the Western Long-tailed Hermit in Costa Rica. Although most of the population in one study moulted at the same time in different years, moult cycles of several individuals were as much as six months out of phase. Furthermore, the study, by F. G. Stiles and L. L. Wolf, revealed that at the individual level there was no consistent temporal relationship between moult and the onset of breeding. Males occupied lek territories during much or all of their moulted period, while some females interrupted their slow moult for



A characteristic feature of hummingbird plumage is the iridescent colouring present in many species. Unlike the coloured feathers of most birds, iridescence is a physical, rather than pigment-related, property. Beneath the upper surface of platelets in the feather barbules is another layer comprising air-filled melanin bodies. When light is reflected from this double surface, it is neutralized by interference allowing other wavelengths to stimulate colour vision. The plumage of most hummingbirds is usually green or blue, or a combination of these as in the Purple-crowned Woodnymph.

[*Thalurania colombica colombica*, Santa Marta, Colombia. Photo: Luis Mazariégos]

The Blue-throated Starfrontlet has a coppery vent, bright purple belly, green breast and head with a bright blue throat, when viewed from appropriate angles. The wing feathers are quite dull, however. Iridescence tends to be restricted to body or tail feathers of hummingbirds, as the design of shining feathers precludes the presence of hooklets between barbules, which in turn reduces the mechanical strength of the feather.

[*Coeligena helianthea helianthea*, Laguna Chingaza, Cundinamarca, Colombia. Photo: Luis Mazariégos]



Hummingbirds are famed for the startling beauty of their plumage.

In general, this gaudy attire is exclusive to males, as their mates carry the burden of parental duties. While incubating and feeding young, they rely on crypsis as a defence against predation. Males are less constrained by predation costs and have developed fabulous coloration, which functions in various communication systems. During territorial or courtship displays these plumage traits are used as cues to signal identity, dominance and quality.

As the physiological production of iridescent plumage is theoretically costly, shiny plumage might act as an honest signal of individual quality, with poor males unable to meet the cost of production and therefore easily recognized by potential mates.

Iridescence is most frequent in territorial hummingbirds of well-lit habitats while non-territorial denizens of dark understoreys, such as the Phaethornithinae, often lack iridescence.

Amongst the brightest members of the family are the Green-crowned Brilliant, the Crimson Topaz and the Ruby-topaz Hummingbird. The moult of brightly coloured body feathers often occurs several weeks after the replacement of flight-feathers, perhaps to ensure that they are in prime condition at the outset of the breeding season.

[*Heliodoxa jacula henryi*,
Costa Rica.
Photo: Michael Fogden/
Oxford Scientific Films.

Topaza pella pella,
Burro Burro River,
Guyana.
Photo: Doug Wechsler/
VIREO.

Chrysolampis mosquitus,
Cauca Valley, Colombia.
Photo: Luis Mazariegos]



breeding. The researchers concluded that a moult-breeding overlap enables the species to reproduce at any time when environmental conditions, such as food supply, are most favourable.

The degree of individual variation and the differences during annual hummingbird moult sequences suggest a genetic or physiological moult-site initiation adjusted to temporal variables and local effects rather than a predetermined, genetically fixed rhythm for each feather follicle.

Nectar supplies the necessary energy for the highly evolved muscular system of trochilids. Hummingbirds take up nectar using their extendable bifurcated tongue, which is forced out of the bill by the hyoid apparatus stretched around the posterior part of the skull. The proximate half of the muscular tongue is partly cartilaginous. The distal half is divided lengthwise, forming two separate membranous curled troughs. This frontal part is essential in nectar drinking, since the liquid nectar is carried into the external troughs by capillary action. The amount of liquid food taken depends on the size of the distal troughs, which increase linearly according to tongue length. In the Ruby-throated Hummingbird each groove may hold up to 0.4 microlitres. It has been shown experimentally that during nectar consumption the grooves on the hummingbird tongue may play only a minor role when large volumes of nectar are available, but they are of importance for emptying small volumes of nectar in flowers. The rate of tongue licking varies from 3 to 13 licks per second. In nature, corolla curvature, position, and nectar volume are important factors in determining nectar extraction rate from flowers. As a general rule, hummingbirds drink their body mass of nectar in several hours.

The exact functioning of the upper and lower mandibles in drinking is not fully understood. One suggestion is that the liquid-filled tip of the tongue is actively emptied by bill constriction, or that the nectar is squeezed from the capillaries by stretching the tongue partly out of the slightly opened bill. Probably both actions are operative.

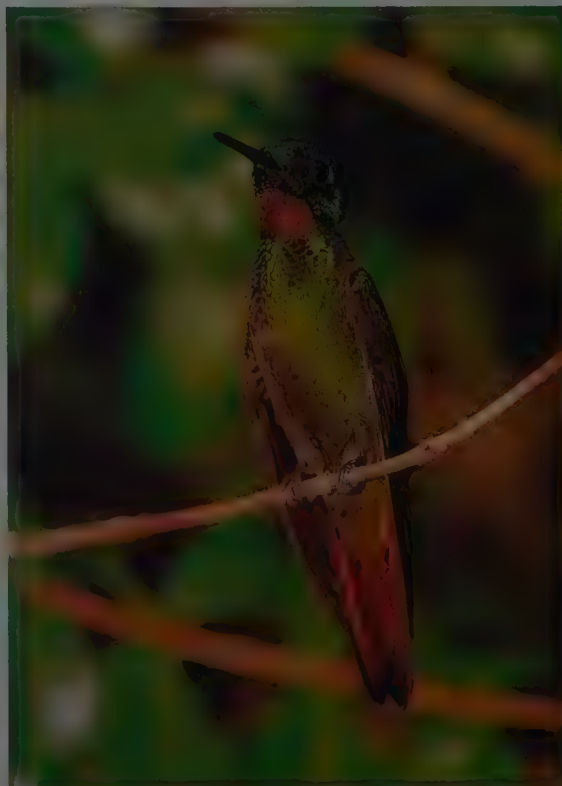
The first ornithologists to study hummingbirds supposed that the forked tip of the tongue had a sticky surface working as a glue to trap insects. However, this nectar-specialized feeding apparatus is completely unsuited for the capture of insects hidden inside flowers. Insects providing most of the protein in the hummingbird diet are caught by hawking, or by gleaning from vegetation or from spider webs. Hawking is common in short

and straight-billed species, whereas long-billed species like hermits (Phaethornithinae), incas and starfrontlets (*Coeligena*) are specialized insect gleaners. In many species like the coronets (*Boissonneaua*), metaltails (*Metallura*) and trainbearers (*Lesbia*), both methods can be observed.

Nectar also supplies the necessary energy for growth and renewal of body tissue, maintenance of body temperature at 40–42°C (endothermy) and other important biological functions including reproduction. Since hummingbirds have the highest mass-specific basal metabolic rates of all birds, their digestive system is well adapted to break down food as quickly as possible and to absorb the nutrients contained therein.

The alimentary system consists of the buccal apparatus, comprising the bill, the mouth with rudimentary salivary glands and a few taste buds, and the tongue. Another sub-unit consists of the oesophagus and the crop, a sac-like thin distension where solid food (insects, spiders, pollen) is moistened and softened with mucus. A specific feature in trochilids is the proximity of the entrance of the first stomach section to the exit of the second. Nectar therefore immediately reaches the short small intestine where it is absorbed. Only solid food particles enter the first part of the stomach, the proventriculus, where they are mixed with more mucus, hydrochloric acid and pepsin. Here begins the digestion of protein, to be continued in the second part of the stomach, the ventriculus, where muscular contractions ensure the necessary mixing of the pepsin with its substrate. In trochilids the ventriculus is smaller than the proventriculus. From the ventriculus food passes to the short small intestine, the duodenum and ileum, where liver bile and pancreas enzymes contribute to the main phase of chemical digestion. Nutrients are absorbed quickly by intestinal tissue and released to the bloodstream. Indigestible material is passed on to the reduced large intestine (colon and cloaca) where water reabsorption takes place before faeces are secreted together with urine via the cloaca.

The carbohydrate-rich sugars of the nectar are passed directly to the small intestine, without entering the stomach, where they are quickly digested. The intestinal transit time is often less than 15 minutes. In this short time hummingbirds succeed in extracting up to 99% of the ingested sugar glucose. This is possible because of the very high number of glucose transporters per quantity of intestinal tissue, most likely the highest number in all vertebrates.



Not all hummingbirds are bright, and some, such as the Buff-breasted Hummingbird of northern Colombia and Venezuela, are inexplicably dull.

This species inhabits arid thorny scrub and subdesert habitats, foraging on the flowers of xerophytic plants such as Agave and Opuntia. As congeners that inhabit forest are considerably more colourful, it has been postulated that brightness may be environmentally mediated, and less likely to occur in bleak or open situations. This relationship does not hold true in all genera, however.

[*Leucippus fallax*, Riohacha, Guajira, Colombia.
Photo: Luis Mazariagos]

Amongst the most frequent plumage signals in the family are the glossy facial markings of many males. The male Brazilian Ruby, for example, develops a violet throat patch and an iridescent green forehead, whereas females are uniformly rufous below and duller above. This species is restricted to south-eastern Brazil where it is common, tolerating disturbed habitats, attending hummingbird feeders around major cities such as Rio de Janeiro, and occupying territories in the understorey of humid forests.

[*Clytolaema rubricauda*, Espírito Santo, Brazil.
Photo: Luiz Claudio Marigo]



One of the interesting features of iridescence is the variability of perceived colours according to the angle from which feathers are viewed. The frontal "visor" of this male Hyacinth Visorbearer, for example, appears black when viewed from the side, but turns shining green when the head turns towards the observer.

This has the added advantage of being a focused signal, "switched on" when the bird faces an intended recipient, and "switched off" when it chooses to look away, perhaps a factor underlying the prevalence of facial iridescence in the family. This species is restricted to central Brazilian hills and plateaux, where it abounds locally in low vegetation, feeding at flowering bromeliads and cacti.

[*Augastes scutatus*,
Sierra de Piedade,
Minas Gerais, Brazil.
Photo: Luiz Claudio
Marigo]

It takes about four minutes for a hummingbird to empty its crop of a nectar meal into the intestine. Crop-emptying is in turn limited by the ability of the intestine to absorb the nutrients contained in the nectar. It has therefore been suggested that the density of glucose transporters in trochilids is the maximum structurally possible for any intestinal membrane. Digestive physiology obviously limits the feeding rate of hummingbirds, just as it does in ruminants like cows, though for very different reasons.

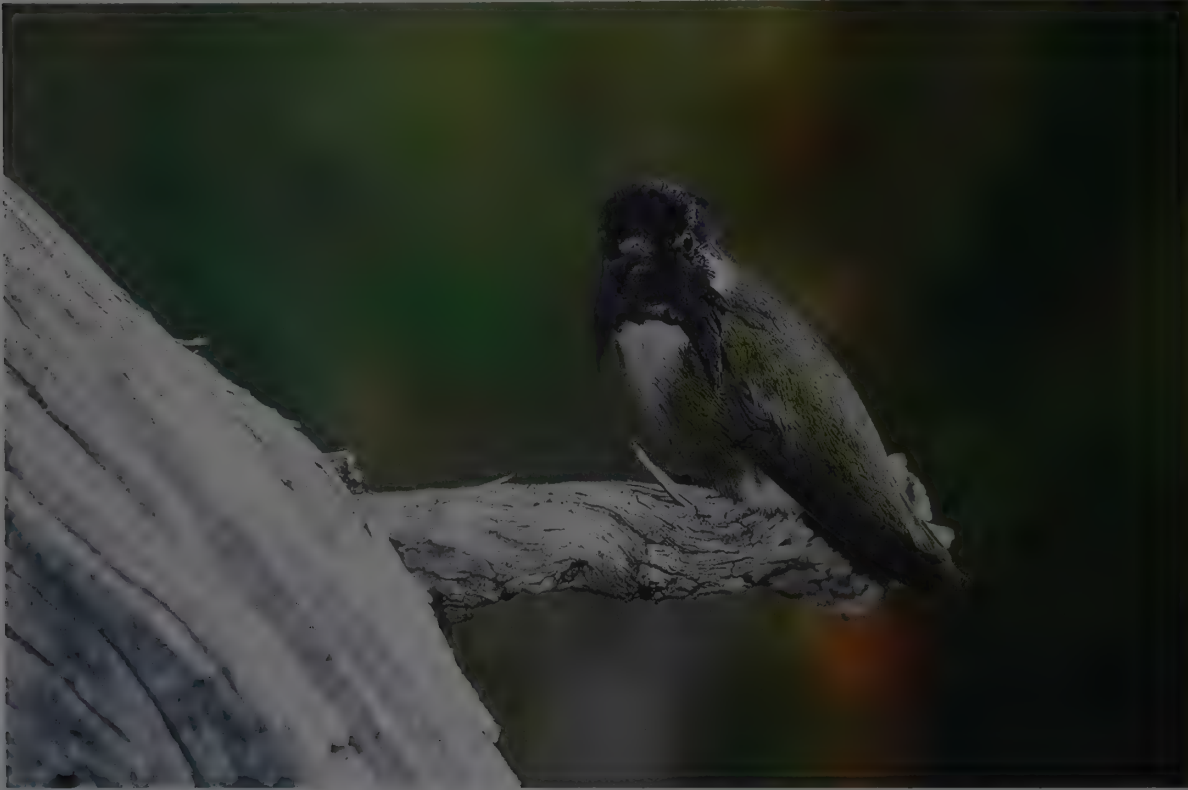
Unlike many other birds, hummingbirds have no caeca; these are short projections of the large intestine that provide a further bacteriological digestion of nutrients. Caeca are common in birds feeding primarily on plant material, like galliforms, which degrade plant particles to volatile fatty acids by means of bacteria. A further anatomical peculiarity of those trochilids studied so far is the absence of a gall bladder.

The liver of hummingbirds is able to store large quantities of lipids and glycogen. In species like the Ruby-throated Hummingbird, these important energy reserves account for 45% of total liver mass at the beginning of migration. In non-migra-

tory tropical species liver lipid reserves amount to about 6% of their mass.

Due to their energy-demanding hovering flight, hummingbirds have the highest oxygen requirements of all vertebrates. Their respiratory system, two compact symmetrical lungs for gas exchange and nine thin-walled air-sacs acting as bellows for their ventilation, is adapted to utilize high gas volumes. At rest, the breathing rate is 300 times per minute, which may rise under heat conditions or during hovering flight to over 500 per minute, whereas a starling or a pigeon breathes roughly 30 times per minute, and man about 14-18 times per minute. The tidal volume of each respiration act ranges in trochilids from 0.14 to 0.19 cm³, which is 100% higher than in mammals of similar size (shrews).

Air enters the body through two nostril slits at the proximate part of the maxillary, flowing to the nares and the pharynx, entering the glottis at the base of the tongue into the upper end of the windpipe, or trachea. The glottis has a long slit without a protective cartilage flap and is compressed by rapid reflex movements, preventing solid particles from entering the



Investigation has shown that hummingbirds' eyes possess a visual pigment which is sensitive to ultraviolet (UV) light. This might be especially important in identifying rich nutrient sources, especially as flowers in their fertile phase are known to exhibit UV-specific colour patterns. Moreover, as the spectral reflectance of iridescent plumage includes UV wavelengths, glossy plumage signals may be even more conspicuous to hummingbirds than they are to humans. Male Costa's Hummingbirds vigorously defend territories encompassing flowering shrubs, often using regular perches from which they scan for potential mates and intruders, and sally after flying insects.

[*Calypte costae*,
Sonoran Desert,
Arizona, USA.
Photo: Günter Ziesler]

trachea. The trachea channel consists of cartilaginous rings, with fibrous tissue in between, providing the necessary flexibility during locomotion. When passing through the wishbone the trachea bifurcates into two tubes, the primary bronchi, each of which goes to one lung. These then give rise to the first set of secondary bronchi on the backward side of the lungs, spreading over the ventral surface and transporting air to the cranial air-sacs. The primary bronchi continue to the lower backward

side giving off a second set of secondary bronchi, which spread out over the inner surface of the lung. At the caudal lung margin the primary bronchus ends in the abdominal air-sac. The sets of secondary bronchi are connected to capillary vessels where the gas exchange takes place.

Respiratory movements in trochilids and most other birds are independent of flight movements. They are produced by the rib and abdominal wall muscles, which are isolated from the large flight muscles. These discoveries have been made by recording wingbeats and breaths and noting different relationships between them, ranging from 3:2 to 5:1.

Like most avian groups, trochilids depend on their eyes while flying, and rely on vision for finding food sources or for recognizing predators, food competitors, and mates. Since hummingbirds are diurnal their sight is more developed for daytime activities. Their globose eyes are on the sides of the head, which increases the visual field, allowing monocular and binocular vision. In general, the anatomical structure of the hummingbird eye is similar to that of other birds.

The two photoreceptors, the rods and cones, contain the visual pigments responsible for the absorption of light incident upon the retina. Rods are sensitive to colourless and dim light, whereas cones are receptive to colour vision. The three cone pigments are sensitive to red, green and blue light respectively (trichromatic colour vision). Behavioural studies indicate that, like pigeons and other birds, trochilids may have a fourth cone visual pigment that is sensitive to ultraviolet light between 325 and 360 nanometres. Since many flowers bear UV-specific colour patterns of changing sizes during their fertile phase, when high nectar rewards can be expected, hummingbirds may use these cues to locate food.

Among all birds, songbirds are considered to have the most highly specialized brains; their encephalization factor is 5.4 compared with the galliforms. In hummingbirds this figure is 2.5, still clearly smaller than in passerines. Though trochilids are intermediate, they can be considered as highly encephalized. The relatively high encephalization factor in hummingbirds can be interpreted in two ways: either the brain is relatively large with respect to the body, or the body is relatively small with respect to the brain. Probably the first assumption is more likely. Although hummingbirds are very small, it has been shown that even



The Rainbow-bearded Thornbill earns its name from a multicoloured strip of iridescence on the head of males. An emerald-green throat patch extends onto the chest as a fiery red strip and onto the crown as a yellow cap. In females, the extension of red is much reduced and the crown is largely rufous. This species frequents high altitudes in the Andes, where it feeds on the nectar of páramo plants, often perching rather than hovering, and it spends a large proportion of its time hunting insects on or close to the ground.

[*Chalcostigma herrani*
herrani,
Caldas, Colombia.
Photo: Luis Mazariegos]

an extremely small body size does not necessarily lead to an increased encephalization index. At the same time, the unique and complex behaviour of hummingbirds allows them to use their ecological food niche almost exclusively, demanding a highly specialized sensorimotor control (hovering) by the brain. It remains unknown which type of encephalization hummingbirds have undergone as there is no information on volumes of different structures of the brain. It has been suggested that this high encephalization factor is not only due to an enlargement of the forebrain but also in part to cerebellar and/or brain stem specializations.

Nectar preference tests show that foraging hummingbirds have control mechanisms at their disposal which allow them to regulate energy costs and benefits over time in order to build up the energy surplus necessary for their nocturnal resting phase. The quantitative proof leads to a clear evaluation of the energetic cost-benefit balances. They are ultimately determined by intercellular reactions whose catalysing function is temperature-dependent. For the optimal functioning of such chemical processes it is to an organism's advantage to maintain a relatively constant body temperature, within the constraints of its energy balance. This applies to hummingbirds as to most terrestrial endotherms.

The daily energy requirement of a 4-5 g hummingbird lies roughly in the range of 30-35 kJ, which amounts to five times the estimated basal metabolic rate. In order to meet their daily energetic needs hummingbirds have to consume the nectar of about 1000-2000 flowers each day. The estimated daily water intake with the nectar meals amounts to around 160% of their body mass. This significant water excess is eliminated in chronic diuresis, causing a salt-balance problem. Hummingbirds have solved this physiological constraint by having kidneys that contain a poorly developed renal core consisting largely of collecting ducts with only a few looped nephrons, or waste-extracting units. Hummingbirds thus do not concentrate their urine like other birds and mammals, but reclaim valuable salts thanks to a reduced osmotic concentration in the region of 15-24% of plasma concentration. Although 76-85% of the solutes is conserved each day, over 10% of body sodium and potassium is lost. These salts are normally replaced from trace amounts in floral nectars. It has been suggested that the evolution of nectar-feeding in trochilids led to their small body size. Therefore the constraints on kidney size to process this relatively large flow of excess water could only be handled by foregoing nephrons capable of producing concentrated urine (mammalian-type nephrons).

Trochilids are found between Alaska in the north and Tierra del Fuego in the south of the American supercontinent, occupying all types of habitat from sea-level to about 4500 m where flowering plants are available. Over 50% of all species occur in montane regions and are exposed to a daily temperature stress of more than 15°C. For physiologists it was therefore of particular interest to investigate the amount of heat production necessary to offset the difference between ambient and body temperature. If thermal conductance, a measure of physical characteristics influencing heat exchange, is high, then the bird is poorly insulated. One should expect trochilids to be poorly insulated because of their low body mass (in birds, thermal conductance increases exponentially by a factor of -0.5 with decreasing body mass), as well as by the relative small number of feathers covering their bodies. Nevertheless, hummingbirds have very high heat production per gram of body mass. Due to their low mass, their energy requirement for temperature regulation is much less than it is for larger animals. The main problem for small endotherms is to store sufficient energy to compensate for the expenditure involved in thermoregulation. In general, animals store energy in linear proportion to their body mass with a rate of increase of 1.0, but the rate of energy loss increases linearly by 0.75. The energetic problems experienced by very small animals result from the differences between these parameters. Thus, small endotherms like hummingbirds are under considerable time pressure: on the one hand they must meet their daily food requirements; and on the other, accumulate sufficient energy reserves to survive their nocturnal starvation. The following factors are therefore of decisive importance for extremely small hummingbirds: quality and accessibility of food; and mechanisms to reduce energy consump-

Many hummingbirds show patches of white that offset the brilliance of iridescent plumage. In particular, members of the genus *Heliangelus* are often characterized by the presence of white collars, as can be seen here in the male *Gorgeted Sunangel*. A hovering hummingbird has the highest oxygen demand of any vertebrate. At rest, the breathing rate is 300 times per minute, which rises when temperature increases or during flight to over 500 times per minute. In contrast, a resting human breathes roughly 14-18 times a minute and a pigeon around 30 times per minute.

[*Heliangelus strophanus*,
Mindo, Ecuador.
Photo: Luis Mazariegos]

The *Snowcap* is thus named because of the startling white crown feathers of males. This feature is very conspicuous against a background of dark iridescent plumage, and presumably performs a similar function to the iridescent crowns of other species which contrast with duller or differently coloured plumage. It lives in the lowland and foothill forests of Central America, where it forages at the small flowers of trees, such as *Warscewiczia*, shrubs, vines and epiphytes.

[*Microchera albocoronata*
parvirostris,
Costa Rica.
Photo: Michael &
Patricia Fogden]



tion. In trochilids, these mechanisms are long periods of inactivity between daily meals and torpor.

During torpor, gaseous metabolism and body temperature are adjusted to the levels of ambient temperature and regulated to remain within the range of 18-20°C. In torpor, hummingbirds become lethargic and incapable of reacting in a coordinated way to external stimuli. Energy savings during this immobile state are considerable; up to 60% of the total energy accumulated for the nocturnal resting phase. During observations on Nearctic migratory hummingbirds an irregular occur-





rence of torpor was noted. Birds reacted only with torpor when energy levels fell below lower limits during the night. According to these studies, torpor is an energy-regulating mechanism which is triggered below a threshold value, equivalent to a physiological regulation pattern coming into force in extreme conditions. As reasons for the irregularity of torpor, physiologists cite the risks and energetic costs of the lethargic state. The risks involved would be the danger of predation while immobile, and insufficient residual energy for thermoregulation which could prevent awakening from torpor.

Recent research on Neotropical trochilids from a wide range of climatic zones and altitudes shows that in all species torpor occurs nocturnally. There are two distinct metabolic phases: during the night, metabolism is lowered by 80-90% of the daytime value for 2-6 hours, then, still in morning darkness, endogenously levels off in two different plateaux of regulation to normal activity. Torpor was noted in all ambient temperatures tested experimentally, from 5°C to 25°C, independent of taxon and body mass.

If a hummingbird was exposed to temperatures below 15°C the resulting body temperature was regulated to remain in the range of 18-20°C. This regulated reduction of metabolism and body temperature was accompanied by a drastic lowering of the heart rate to 50 beats per minute, and a reduction of the breathing rate by about 50% compared to activity levels. These results suggest that torpor in Neotropical hummingbirds occurs regularly as an energy-controlling system. Torpor duration and depth can vary depending on the size of the energy reserve accumulated during the previous day. It has been suggested by several ornithologists that torpor is a phylogenetically derived energy-saving mechanism in groups of endothermic organisms that occasionally (some pigeons and songbirds, mousebirds) or permanently (hummingbirds, shrews) live at the limit of their energetic existence. Torpor has an important additional function for these vertebrates because body temperature and metabolism are adjustable at any required energy level. The hypothesis that torpor is an acquired secondary character in the above vertebrates is supported by the fact that hummingbirds and shrews exhibit endothermy only at an age of at least one week.

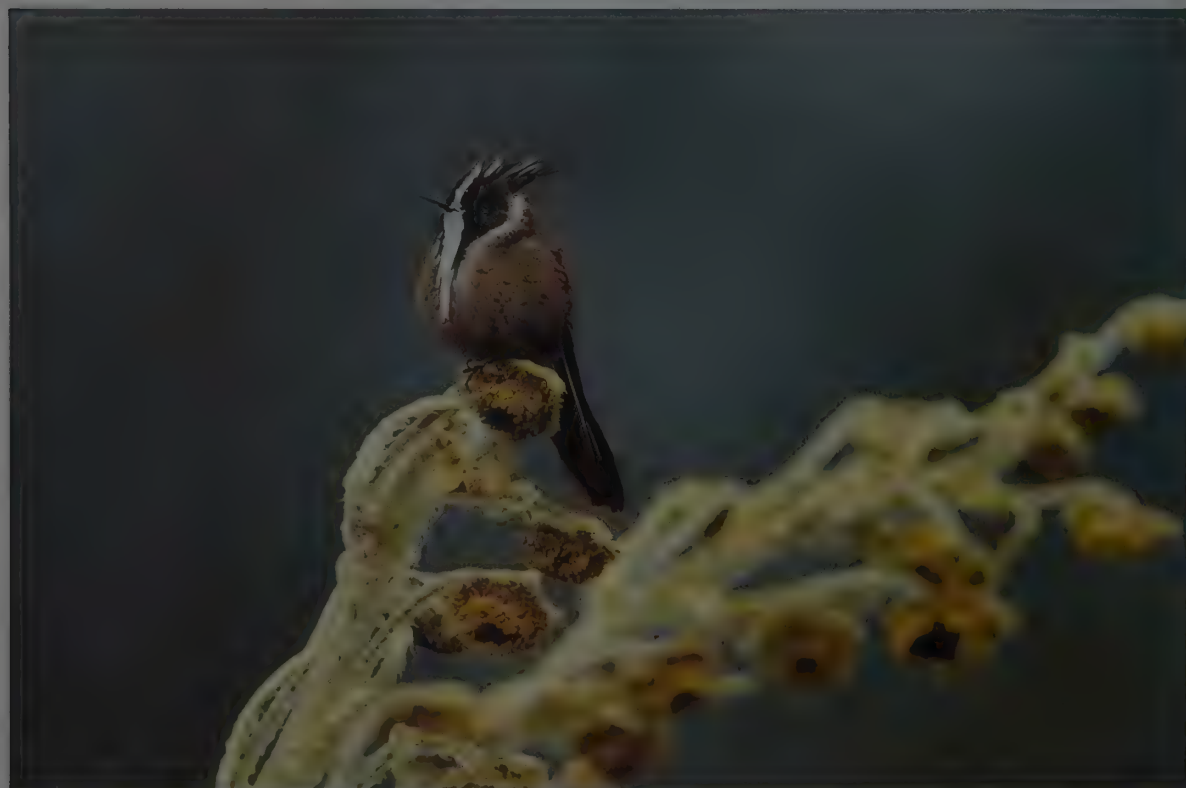
Regular occurrence of torpor has not been observed in Nearctic hummingbirds. An explanation could be that these trochilids enjoy long daylight conditions of 14-16 hours in their northern summer quarters during which to feed, resulting in a positive energy balance. Changes in levels of metabolism and body temperature only occur when the lower energy balance threshold is crossed.

Habitat

Hummingbirds live in an extremely wide range of New World habitats. Some species like the helmetcrests (*Oxygogon*) in western Venezuela and Colombia, and the hillstars (*Oreotrochilus*) from Ecuador south to Chile, can be encountered at over 4000 m on the verge of Andean snowfields and glaciers, where in wind-sheltered and sun-exposed canyons a relatively species-rich community of bird and insect-pollinated alpine flora flourishes. These high-altitude trochilids forage among dense stands of year-round flowering Scrophulariaceae, Asteraceae (Compositae) and Gentianaceae, which provide nectar, their essential energetical

In many hummingbird species visual signals are not restricted to patches of bright colour, but include modified tail feathers or head feathers. The male Plovercrest has a long plume extending from its crown. The two forms of this species have different coloured crests: greenish in the race *lalandi* and bluish in *loddigesia*.

[*Stephanoxis lalandi lalandi*.
Photo: C. H. Greenewalt/
VIREO]

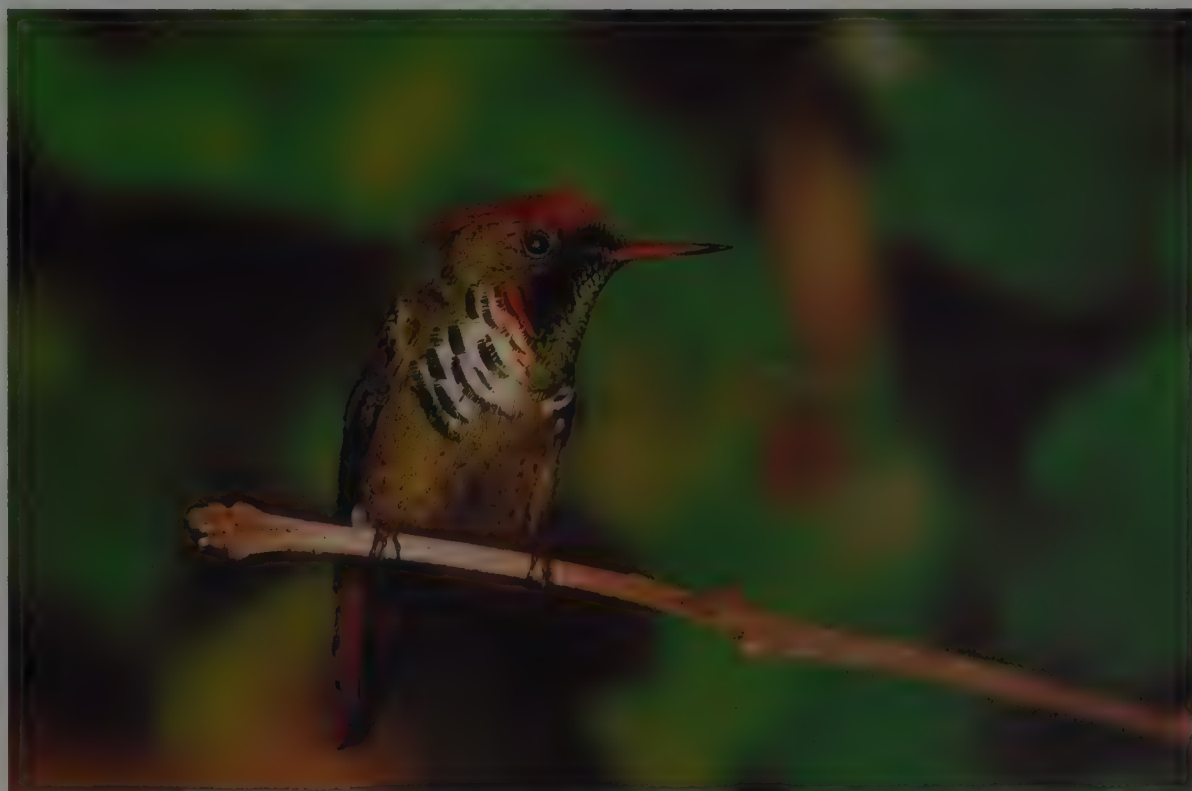


At around 4000 m, beside the glaciers and snowfields of the Andean cordilleras, night temperatures fall well below zero and blizzards are regular. The fact that the Bearded Helmetcrest and members of *Oreotrochilus* are amongst the few birds that can survive there is testament to the resilience and adaptability of the family. Only when snow cover is comprehensive do they descend a few hundred metres to the sparsely vegetated upper páramo, returning to higher altitudes when conditions improve. As a result of their adaptation to this extreme habitat, they enjoy reductions in both predation and competition for resources, since potential predators and competitors are scarce.

[*Oxygogon guerini lindenii*,
Páramo La Culata,
Venezuela.
Photo: Thomas Züchner]

The Frilled Coquette is an inhabitant of forests and secondary growth in the lowlands of Brazil and Bolivia. Its shining throat is enhanced by a suite of secondary signals, including cheek tufts and a crest which can be raised during display. Coquettes are often "territory parasites", feeding at profitable patches defended by larger, more aggressive species. They pursue this strategy surreptitiously by frequenting inconspicuous locations, avoiding territory owners and acquiring resources without physically competing for ownership of the patch.

[*Lophornis magnificus*,
Espírito Santo, Brazil.
Photo: Luiz Claudio
Marigo]



fuel, and attract the insects that supplement their diet. Nocturnal frosts, occasional snowstorms, and daily temperatures of a few degrees above zero are the environmental conditions in these Andean regions. Helmetcrests and hillstars rarely leave this alpine habitat, except for periods of longer snow cover. Then they shift to the upper *páramo*, an open grass-dominated vegetation with scattered stands of small trees and shrubs, only a few hundred metres below their native habitats. Often they leave the *páramo* plateaux again after a few hours and return to the rocky heights when weather conditions are favourable again. During frosty nights, trochilids of alpine Andean regions seek shelter in caves, commonly found below the snowfields of volcanoes, or under overhanging vegetation on the steep slopes above mountain streams or ravines. The members of these two hummingbird genera have evolved in such a way that the only habitats they are able to occupy on a regular basis are the extreme environments of the high Andes. Here they are physiologically well adapted, they reproduce successfully without facing strong competition for nesting sites and food from other trochilids, and, equally importantly, they are not exposed to predation.

At slightly lower elevations, between 3000 and 3800 m, a grassland zone forms the characteristic vegetation. Whereas the high Andes of Venezuela, Colombia and Ecuador are cool and damp, the Altiplano of Peru and Bolivia is characterized by being cool and dry.

Penetrating drizzle, sometimes turning into snow, and a constant dense fog cover, leaving everything dripping wet, is the characteristic weather of the Andean *páramo*, known from Ecuador north to western Venezuela. Although grass tufts carpet the ground at these altitudes, numerous taller herbaceous plants form the typical landscape, like the man-sized giant *Espeletia* (Asteraceae), locally called *frailejones*, with typical rosette-like broad whitish hairy leaves, and terrestrial bromeliads of the genus *Puya* (Bromeliaceae), with huge cone-shaped inflorescences consisting of hundreds of single flowers. Besides these more obvious typical *páramo* plants, a large number of other herbaceous flowers and woody plants, all several metres high, belonging to many different families, including Rosaceae, Myrtaceae, Ericaceae and Melastomataceae, often occur in wind-sheltered ravines. In this border zone between small patches of forest thickets and open *páramo*, members of over half a dozen trochilid

taxa occur all year round, albeit at varying densities, namely species of the genera *Aglaeactis*, *Chalcostigma*, *Metallura*, *Ramphomicron*, *Lafresnaya*, *Eriocnemis*, and sometimes *Chaetocercus*. Some species like the Purple-backed Thornbill are stragglers, or, in the case of the Shining Sunbeam (*Aglaeactis cupripennis*), local migrants in parts of their range. During the major flowering period from the end of June to August, many more hummingbirds from lower elevations temporarily visit the *páramo* due to the superabundant nectar supply in the dense stands of angiosperms, plants which are in turn dependent on trochilids for pollination. Then large numbers of Sparkling Violet-ears from the lower Andean valleys, and occasionally, during warmer sunny days, even Green Hermits (*Phaethornis guy*) from the upper tropical rainforest may be encountered on the *páramo*. However, these species disappear in the afternoons, obviously returning to lower elevations again.

The mostly dry and windy *puna* zone of the Peruvian and Bolivian Andes is less favourable for hummingbirds than the northern wet *páramo* at similar altitudes. In the *puna*, trochilids are much more confined to edges of *Polylepis*-*Gynoxys* woods and to sheltered gulleys with bushy vegetation, than to open grassland. The Giant Hummingbird and the Andean Hillstar (*Oreotrochilus estella*) occur regularly in the open grasslands of the southern high Andes mainly during the flowering period of the arborescent puya *Puya raimondii*. A typical open *puna* species, the Olivaceous Thornbill (*Chalcostigma olivaceum*), frequently perches on grass tussocks from where it sallies forth for flying insects. However, most of the hummingbirds at this altitude are found around the edges of *Polylepis* forest and stands of composite shrubs, Scrophulariaceae (*Castilleja*), and cacti (*Opuntia*) flowers, which supply energy-rich nectar, the prerequisite for remaining sedentary at these climatically hostile altitudes.

At 3500 m, the *páramo* and *puna* are sharply replaced by shrubs and trees of the upper Andean forest. Where the two habitats merge, the hummingbird community comprises almost a dozen sympatric species foraging for nectar from a highly diverse ornithophilous angiosperm assemblage, comprising many taxa of vines, shrubs and woody plants such as *Bomarea*, *Fuchsia*, *Lobelia*, *Passiflora*, *Brachyotum*, *Befaria* or *Datura*, with brightly red- or orange-coloured tubular flowers, a major visual



The White-tailed Starfrontlet, endemic to the Santa Marta Mountains of northern Colombia, shows remarkable contrast between dark body plumage and a white tail, a contrast particularly visible in the gloomy understorey of the forests it frequents. As a general rule, hummingbirds drink their body mass of nectar in several hours, thus supplying the necessary energy for growth and maintenance of body temperature at 40°-42°C. As hummingbirds have the highest mass-specific basal metabolic rate of all birds, their digestive system is adapted to maximize the speed with which nutrients are metabolized and absorbed.

[*Coeligena phalerata*, Santa Marta, Colombia. Photo: Luis Mazariegos]

cue for their minute avian visitors. From Venezuela to the Yungas of Bolivia this life-zone forms the upper distribution limit of the Sword-billed Hummingbird, a little-studied specialist of long-tubed pendent flowers, with the longest bill of all trochilids, up to 12 cm long. Another large hummingbird occupying the same habitat is the Great Sapphirewing (*Pterophanes cyanopterus*), as well as other closely related long-billed allies from the inca and starfrontlet group (*Coeligena*), together with pufflegs (*Eriocnemis*) and sunangels (*Helianthus*). Whereas the *Coeligena* assemblage occupies forest edge and forest interior habitats from low-growing shrubs to the subcanopy of trees, the pufflegs and sunangels of that altitude are more restricted to the buffer zone of shrubs between the semi-open sub-*páramo* and the upper Andean forest belt.

The richest altitudinal zone in terms of hummingbird species is the transitional zone between the Andean forest and the adjacent

lower submontane forest, roughly between 2500 m and 1800 m. Here the daily temperature is fairly constant, ranging around 12-16°C. Daily cloud cover, especially in the afternoon, brings the moisture that sustains a rich plant life of ferns, shrubs, trees, vines and especially epiphytes, like orchids, bromeliads, gesneriads and ericads. As diurnal endotherms, trochilids are the most successful organisms serving the cloudforest plants as pollen vectors. At these altitudes, heterothermic insect pollinators are dependent on favourable temperature and weather conditions, which limits their flight activity to a few, often unpredictable daytime hours.

Although there is some flowering seasonality among ornithophilous plants of different families like Ericaceae and Rubiaceae, this Andean life-zone between 12° north and south of the equator provides abundant nectar all year round, allowing the co-existence of over a dozen hummingbird species. The cloudforest trochilid community comprises a concentration of very small to medium-sized and large species from about 3 to 12 g, with diverse bill shapes and sizes. If we list body size and bill shape of typical members of the Ecuadorian cloudforest trochilid assemblage, an impressive picture can be gained of the variety of niche exploitation possibilities: the Booted Racquet-tail has a tiny body, and the bill short and straight; the Purple-bibbed Whitetip (*Urosticte benjamini*), small, and straight; Speckled Hummingbird (*Adelomyia melanogenys*), medium-sized, and short; Hoary Puffleg (*Haplophastura lugens*), small, and short; Wedge-billed Hummingbird (*Agastis geoffroyi*), small, and short and conical; Andean Emerald (*Agyrtia franciae*), medium-sized, and straight; Green-fronted Lancebill (*Doryfera ludovicianae*), medium-sized, and long and straight; Violet-tailed Sylph (*Agelaiocercus coelestis*) medium-sized, and short and straight; Tawny-bellied Hermit (*Phaethornis symrathus*), large, and long and decurved; Brown Inca (*Coeligena wilsoni*), large, and long and straight; Buff-tailed Coronet (*Boissonneaua flavescens*), large, and long and straight; White-tailed Hillstar (*Urochroa bougueri*), very large, and short and straight; Fawn-breasted Brilliant (*Heliodoxa rubinoides*), large, and short and straight; and Brown Violet-ear (*Colibri delphinae*), medium-sized, and short and straight. Alongside these core species another 10 to 15 hummingbird taxa may be found in the cloudforest during the peak of the flowering season, attracted by the nectar-rich ericad shrubs and *Inga* trees. These trochilids comprise various lowland spe-

The tiny Tyrian Metaltail is an inhabitant of the magnificent Andean highlands from Venezuela to Bolivia, occupying both sides of the ecotone where páramo and elfin-forest meet. It is commonest above this rather abrupt divide, frequenting moist páramo grasslands that are often smothered in fog and drizzle. With its tiny bill it sips nectar from the inflorescences of terrestrial bromeliads and the innumerable flowering shrubs that grow in this zone.

[*Metallura tyrianthina* tyrianthina, Cauca, Colombia. Photo: Luis Mazariegos]

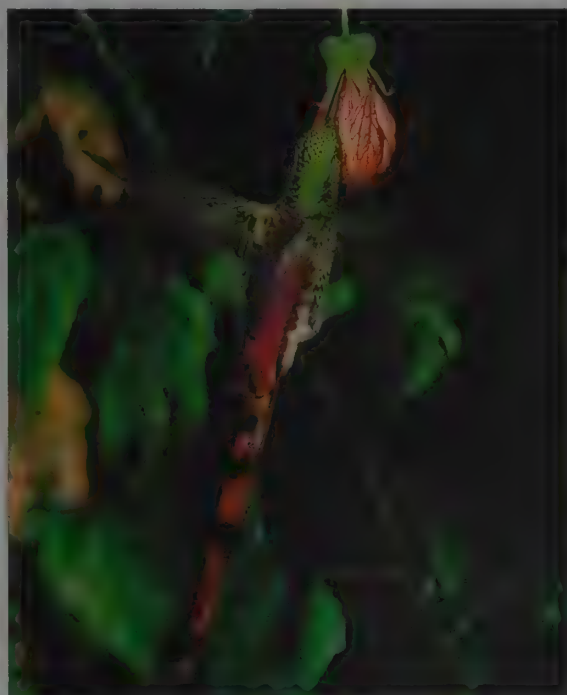


cies like the minute Green Thorntail (*Discosura conversii*) and the much larger White-necked Jacobin (*Florisuga mellivora*), as well as members of high-Andean guilds such as the large Sparkling Violet-ear and the tiny White-bellied Woodstar.

The tropical lowland forests of South America, in stark contrast, harbour a much impoverished hummingbird community. Dominant species of this life-zone mostly belong to the subfamily Phaethornithinae (*Androdon*, *Eutoxeres*, *Glaucis*, *Threnetes* and *Phaethornis*), whereas trochilines are normally represented by the genera *Amazilia*, *Polyerata* and *Agyrtria*, and by *Hylocharis*. The first of these two groups is represented west of the Andes by the Rufous-tailed (*Amazilia tzacatl*) and Purple-chested Hummingbirds (*Polyerata rosenbergi*), whereas east of the Andes are found the Versicolored (*Agyrtria versicolor*), Glittering-throated and Plain-bellied Emeralds (*Agyrtria leucogaster*). Similarly, in the second group, the Blue-headed Sapphire and Blue-throated Goldentail occur west of the Andes, whereas the Rufous-throated (*Hylocharis sapphirina*) and White-chinned Sapphires are found mainly east of the Andes.

Cis- and trans-Andean hummingbird taxa often constitute allopecies of a superspecies with almost identical ecological requirements. A fine example is provided by the two tropical lowland species of the genus *Heliothryx*, separated in their distribution by the Andes. Along the Pacific coast, the Purple-crowned Fairy (*Heliothryx barroti*) is the sole member of the genus, replaced in the Amazon by its sister species the Black-eared Fairy (*Heliothryx aurita*); these two congeners are very similar in their morphological characteristics. Whereas many lowland trochilids forage at certain foliage heights, the fairies belong to those few hummingbird species making use of the complete vertical stratum, sallying during their search for nectar and arthropods several times a day from near the ground to the highest tree tops.

There are several other lowland trochilids like *Florisuga*, *Anthracothorax*, *Topaza* and *Campylopterus*, but many of these taxa are of local distribution; or require specific habitats within the lowlands such as semi-deciduous forest or savannas; occupy a wide range of altitudinal vegetation zones; seasonally disperse to lower altitudes; or are migrants.



Tropical mangroves play a negligible role in the distribution of trochilids. Only one species, the Mangrove Hummingbird (*Polyerata boucardi*), from Costa Rica, is restricted to these coastal lowland habitats. Others like the Glittering-throated Emerald may invade this vegetation during breeding, but are not found there all year round.

In a few cases it is evident that certain taxa are ecologically replaced by others of similar body mass and morphological features. The best example is the long-billed hermit assemblage.

Conspicuous tails are taken to extremes in hummingbirds such as the male Red-tailed Comet, in which they are not only bright but highly elongated. In females the tail is less spectacular, being shorter, duller and less deeply forked. This species is fairly common throughout its range in Bolivia, Argentina and Brazil, where individuals are commonly glimpsed as a streak of red speeding between feeding patches on open slopes.

[*Sappho sparganura*
sparganura.
Photo: François Gohier/
Ardea]

Many hummingbirds possess very bright tails.

The Golden-tailed Sapphire is one such species, males exhibiting brilliant bronzy-copper rectrices, while females are considerably duller.

It is not clear what function bright tails perform, but they are possibly important in courtship when the males assemble at leks consisting of five to ten individuals. This species occurs mainly in primary and secondary forest at lower altitudes, occasionally defending territories in the absence of more aggressive species. The solitary and non-territorial females, meanwhile, feed at dispersed sites in forest.

[*Chrysuronia oenone*
oenone.
Meta, Colombia.
Photo: Luis Mazariegos]





Above 2500 m they are gradually replaced by the morphologically similar long-billed species-group of the incas and starthroats (*Coeligena*). At altitudes where members of both taxa are sympatric, they compete for the same flowers, but deal with this situation by a vertical niche segregation. Hermits remain closer to the ground when foraging for nectar, while the incas and starthroats visit flowers from the middle storey to sub-canopy level.

Hummingbirds occur in many other life-zones including: arid scrub, home of the Lucifer Hummingbird (*Calothorax lucifer*) and the Peruvian Sheartail (*Thaumastura cora*); desert oases, the Oasis Hummingbird (*Rhodopis vesper*); Nearctic pine forests, with many North American species including the Broad-tailed and Magnificent Hummingbirds; and on remote islands in the Caribbean (*Trochilus*, *Chlorostilbon*, *Eulampis*, *Mango*, *Orthorhyncus*) and on the Juan Fernández Islands off Chile, where the Green-backed (*Sephaniodes sephaniodes*) and Juan Fernandez Firecrowns are found. However, many of these habitats are occupied only sporadically for a short period or seasonally during the breeding period, when foodplants are in flower, often providing superabundant nectar. Birds leave these regions again when conditions become unfavourable. Many of the North American trochilids then disappear and migrate to their Central American winter quarters. The same is true for the Green-backed Firecrown, from Chile, which leaves its southernmost summer range on Tierra del Fuego to migrate northwards to western Chile and Argentina. On larger islands, hummingbirds show altitudinal migration or disperse to different lowland habitats.

Where several species of hummingbird co-exist in the same habitat they would be expected to show different body masses and/or bill lengths to reduce interspecific foraging competition among flower-visitors. And indeed this hypothesis is particularly well supported by the example of the trochilids of the Antilles. Two species, differing in their body mass by a factor of around 2, occur on most of the islands. However, where both species have the same body mass, as is the case of the Antillean (*Anthracothorax dominicus*) and Green Mangos (*Anthracothorax viridis*)

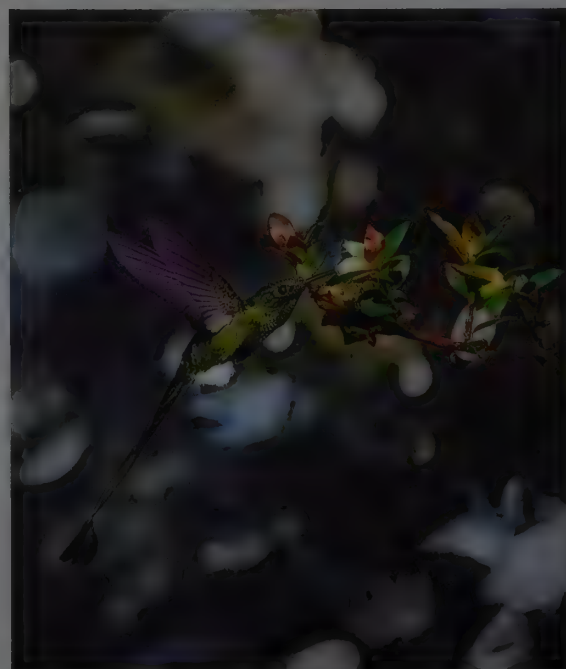
on Puerto Rico, they exclude each other by preferring different habitats. This simple ecological separation is confirmed by looking at the corolla length and nectar production rate of the corresponding food plants. There are two categories: first, corollas 17-20 mm in length, with a nectar secretion rate of 1-2 microlitres of saccharose per day, and with flowers that are visited by the smaller short-billed species of hummingbird; and, second, corollas 30-38 mm in length, with a nectar secretion rate of 4-27 microlitres of saccharose per day, and with flowers that are visited by the larger long-billed species. In tropical regions with species-rich hummingbird communities we find not only differing body masses and morphological characteristics but also species-specific foraging strategies.

Trochilid habitat requirements are still poorly understood. Many species exhibit a remarkable adaptability, easily adjusting to man-made habitat changes, or even expanding their ranges if food conditions are favourable, as in Anna's Hummingbird (*Calypte anna*). Others rapidly decline in numbers and face extinction following environmental disturbance, for instance the Hook-billed Hermit (*Glaucis dohrnii*). In addition to habitat changes, there are cases of competition for food, either from congeners, as with the two *Sephaniodes* species in the Juan Fernández Islands, or not, as in the case of the Chilean Woodstar (*Myrtis yarrellii*) with the larger Oasis Hummingbird; such cases must be thoroughly analysed in the future in order to achieve a better understanding of hummingbird community structure and change, essential factors for any successful conservation programme.

General Habits

Physiological adaptations for nectar feeding, and energy regulation patterns resulting from limiting temporal and environmental conditions are fundamental factors for understanding the general habits of trochilids. The utilization of energy-rich nectars most likely fostered strong individual competition for this food source, favouring the evolution of specific maintenance and survival strategies. As a general consequence, males and females of almost all hummingbird species so far studied live solitarily, often aggressively defending nectar sources in the form of flowering shrubs and trees against any potential food competitor. The sexes are polygamous and associate only briefly to fertilize the eggs.

In general, the males of species with bright iridescent colours establish feeding territories at flowering bushes which allow them to cover their daily energy needs. In order to defend their nectar resources they often perch high on nearby exposed branches. These



In some species, the tail feathers themselves are not only bright but also modified in design. The male Red-billed Streamertail provides a perfect example of this phenomenon, one pair of glossy purple rectrices being greatly elongated into a lyre-like shape. This species is restricted to Jamaica where it inhabits virtually all habitats from sea-level up to elfin forest, and densities of up to 12 pairs/km² have been reported in the Blue Mountains. It apparently prefers disturbed or man-modified habitats, being common in parks and suburban areas where it often extracts nectar through the holes made by Bananaquits (*Coereba flaveola*). In forests it also attends fresh Yellow-bellied Sapsucker (*Sphyrapicus varius*) drillings in tree trunks.

[*Trochilus polytmus*, near Kingston, Jamaica. Photo: Robert Tyrrell]

The racquet-shaped appendages of the male Booted Racquet-tail presumably present a slight aerodynamic inconvenience to their tiny bearer. It seems more than likely that modified tail appendages in hummingbirds are analogous to the sexually selected tail of peafowl (*Pavo*): in other words, that their evolution has been driven by female preferences, and that these in turn are associated with the information conveyed by the ability of males to produce these ornaments and to carry the associated handicap.

[*Ocreatus underwoodii* incommodus, La Planada Reserve, Nariño, Colombia. Photo: Luis Mazariegos]

Of all hummingbirds,
the most bizarre tail
design surely belongs to
the Marvellous Spatuletail.

This species is highly
unusual in that it has only
four tail feathers, unlike
the ten of all other
members of the family.
Two of these form long
curled shafts that cross
over behind the body and
carry broad spatules at
their tips. A small
population of this species
inhabits forest edge,
second growth, montane
scrub and impenetrable
Rubus thickets admixed
with *Alnus* trees on the
east bank of the Rio
Utcubamba, northern
Peru. These habitats are
being rapidly eradicated
by the spread of
agriculture and the
demand for fuel, and this
species is thus red-listed
as Vulnerable.

[*Loddigesia mirabilis*.

Photo: C. H. Greenewalt/
VIREO]



serve as vantage points from which predators can be detected with ease or from which the area can be defended against possible intruders, including females, by vocal warning signals and agonistic flights. Often the territory holder first empties the nectar from peripheral flowers to remove or reduce the feeding reward for newly arriving competitors. Trespassers ignoring the threat calls of the territory owner are robustly attacked in flight, sometimes resulting in direct physical combat. An airborne fighting pair may then be locked in strong claw grips, tumbling to the ground like a falling stone. These fights are rarely harmful to the birds but occasionally small featherless areas can be seen on the upperparts as a result of such aggressive encounters.

Male Purple-throated Caribs react differently to territorial intruders and food competitors during the reproductive period. All but their mates are aggressively chased out of the defended feeding area. Incoming females, however, are guarded and allowed to feed prior to mating. A similar function of the feeding territory has been observed in the tiny dimorphic Green Thorntail by K. L. Schuchmann. From December to March, during the breeding period of the species, *Inga* trees begin to flower in south-western Colombia. Then the long-tailed males establish and defend feeding territories in these forest giants. Short-tailed females entering these feeding grounds are allowed to feed on the nectar-rich brush-like white flowers of the trees; both sexes are nectar thieves, hardly contributing to the cross pollination of *Inga* trees. Frequently, males display to individual females and copulate with them while they are in their territory. Male Green Thorntails aggressively attack all possible territory intruders, even much larger trespassing birds like the numerous Tropical Kingbirds (*Tyrannus melancholicus*) gathered around flowering *Inga* trees. Besides females of the Green Thorntail, a small diurnal moth, the white-banded sphinxlet (*Aellopos titan*), similar in size, appearance and flight behaviour to the white-rumped hummingbird, visits the guarded territories. Being almost perfect female mimics to male hummingbirds, they are obviously considered as potential mates, indicated by the displays directed at them. However, because of their fast and unpredictable flights within the densely packed *Inga* flowers, male Green Thorntails quickly lose interest in these female mimics but still continue with their mate-defence behaviour. Hummingbird males direct their agonistic flight manoeuvres especially at Tropical Kingbirds,

which prey on the white-banded sphinxlet. When male hummingbirds were excluded from a flowering *Inga*, predation rate on the moths was over 80%, and individual moths spent only 1-3 seconds at each flower. When such an *Inga* tree was guarded by a Green Thorntail, male sphinxlet predation by kingbirds declined to 20% and most moths spent 4-6 seconds feeding at each flower visited. In the latter case, *Inga* seed production was significantly higher than in a territory without a hummingbird guard. This mimicry relationship between two different animals, a moth and a hummingbird, is an instructive example of the complex inter-related webs of adaptation in the tropics.

Territories are still defended for a while even when the nectar supply diminishes through time. However, as indicated by the behaviour of Anna's Hummingbird in the western USA, when food becomes scarce, song and gorget display directed at food competitors are the primary form of agonistic behaviour, while chases and aerial displays are less frequently observed; it seems most likely that this is a behavioural adaptation to save energy.

Females of a few hummingbird species may hold temporally and spatially limited territories around localized feeding sites during and after the reproductive period. Studies by J. Dorst, K. B. Armitage and M. L. Cody looked at females defending nest surroundings and birds on migration defending a small area at a locally plentiful food source. However, the maintenance of long-term feeding territories is known only for the Fiery-throated Hummingbird (*Panterpe insignis*), a brightly coloured monomorphic species of southern Central America. This type of territoriality reflects the temporal and spatial decline of nectar resources in conjunction with the resident status of the birds. L. L. Wolf, who has studied female territorial behaviour of this species in Costa Rica, suggests that territoriality in trochilids is accompanied by strong selection for sexual monomorphism in plumage coloration, as being advantageous in aggressive encounters, and for sexual similarity in bill length as advantageous for efficient utilization of limited food resources.

Many species in tropical Central and South America do not establish feeding territories but are trap-line feeders on flowers often too scattered to be defended. But between territoriality and trap-line behaviour many more intermediate feeding strategies can be found, depending on flower dispersion, morphology and nectar reward (see Food and Feeding).



The Emerald-bellied Puffleg, along with most other members of its genus, is distinctive in that both sexes sport conspicuous white tufts at the base of the legs. This species is patchily distributed in humid montane forest in the northern Andes, generally feeding on nectar and taking insects only occasionally. As a result of competition for the energy-rich resource, it is often solitary and aggressively territorial, defending flowering shrubs and trees.

[*Eriocnemis alinae alinae*, Putumayo, Colombia.
Photo: Luis Mazariegos]

Despite being under extreme pressure to gather energy quickly, and having developed many obvious behavioural traits for doing so, hummingbirds spend over 70% of their daily activity phase perched, apparently doing little else besides singing, self-preening and sunbathing. In an experimental study on North American hummingbirds, M. A. Hixon and co-workers discovered that most individuals observed fed at around four-minute intervals. This corresponds well with the findings by J. M. Diamond and members of his research group who demonstrated that laboratory-kept trochilids required four minutes to empty their nectar meal from the crop into the intestine; crop-emptying is in turn limited by the ability of the intestine to absorb the nutrients contained in the food (see Morphological Aspects). Because of this digestive bottleneck, hummingbirds are unable to absorb sugar any faster.

Hummingbirds bathe several times a day. Some sit in shallow water and splash like sparrows, others cling to rocks beside waterfalls gathering moisture and spray from above, vibrating their wings and ruffling their body feathers. Hermits and many trochilids hover just above gently flowing forest streams, then abruptly drop into the water, sometimes almost completely submerging the body. These dives are sometimes repeated over several minutes. In addition to waterfalls, other sites also accepted as bathing facilities by several species include forest pools, quiet streams, and large banana and *Heliconia* leaves that accumulate water or dew. Quite often during gentle rains individuals perch on exposed twigs with spread and vibrating wings and fanned tail feathers obviously enjoying their bathing activities.

Sometimes between each bath, or after several dives, birds return to a nearby perch, shake the water out of their body feathers and begin to preen their plumage. Hummingbirds spend extended periods self-preening. Most species use the bill for oiling, cleaning and arranging their feathers. Normally the lower underparts, primaries and secondaries, wing-coverts, the lower upperparts and the rectrices are all preened with the bill. The region of the head and throat is preened using the claws, by lifting the foot up and over the wing. The Sword-bill Hummingbird, however, preens most of the body and tail feathers with its elongated claws, including even parts of the secondaries and primaries.

Hummingbirds do not show flocking behaviour. Individual social contacts are rare but occasionally do occur around supra-

bundant nectar sources and at cave roosting sites, notably in the hillstars (*Oreotrochilus*). Nest aggregations within a few metres are known for the cave-breeding Ecuadorian Hillstar (*Oreotrochilus chimborazo*) and within a radius of 20-30 m for Costa's Hummingbird (*Calypte costae*), the Bahama Woodstar (*Calliphlox evelynae*), the Rufous-tailed Hummingbird and the Crimson Topaz (*Topaza pella*).

Hummingbirds are well known for their constant interest in investigating all kinds of natural and even artificial items, especially when brightly coloured. Many curious stories exist of trochilids examining red plastic markers or even approaching humans wearing brightly coloured shirts or caps. These close inspections by hummingbirds may be explained by their constant need to find nectar sources to satisfy their energetic needs.

Hummingbird foraging behaviour is determined to a large extent by individual perception and memory capability. Field and laboratory studies by G. H. Pyke, conducted with North American Broad-tailed and Rufous Hummingbirds, suggest that these hummingbirds may at least perceive and remember the number of flowers available on an inflorescence, the number of flowers already probed on the inflorescence and the amount of nectar obtained at the present flower.

Many hummingbirds are already active before dawn and late after sunset. A remarkable example is provided by the high-altitude incas and starfrontlets (*Coeligena*), which visit flowers in the early morning hours when it is still dark. Other species still continue to forage for nectar in the evening twilight before disappearing to their roosts. Although hummingbirds are not nocturnal, the night vision of some species seems to be excellent.

Ornithologists have discovered trochilids at their roosting sites on only a few occasions. Their sleeping places are sometimes well protected by leaves, as in the Rufous-tailed Hummingbird, whereas the Long-billed Starthroat (*Heliomaster longirostris*) roosts on the thin exposed twigs of tree tops. The sleeping position of perching trochilids is strikingly similar in all species observed: with both feet on the perch, head exposed, neck retracted, and the bill pointed forwards and upwards. The tiny Wire-crested Thorntail (*Discosura popelairii*) maintains a similar upright sleeping position but the rectrices are stretched forward underneath the bird's body, possibly to achieve a more effective posture for maintaining balance. By contrast, songbirds

on their roosting sites cover the backward-turned head with the shoulder feathers and often perch on one foot.

Hummingbirds are threatened by only a few predators among vertebrates. Camouflaged snakes on *Heliconia* flowers prey on them when they are foraging for nectar, and will also attack them when the birds are brooding. Forest-falcons (*Micrastur*) occasionally capture hermits at their lek sites, and pygmy-owls (*Glaucidium*) may attack them at dawn when the hummingbirds are visiting flowers. Nest robbers like jays (*Corvidae*), toucans

(*Ramphastidae*) and possibly some bats, however, seem to be the major predators, although it should be stressed that this information has been generated only through occasional observations, so the impact of predation on hummingbird populations is almost completely unknown. Whenever a potential enemy is sighted by a hummingbird it is directly approached by rapid diving attacks accompanied by a series of high-pitched warning calls. These alarm signals regularly attract other bird species, which join in the aggressive flight encounters supported by continuous

Hummingbirds undergo a single protracted annual moult, which commences soon after the breeding season. Initially, primary moult proceeds descendantly, from innermost outwards, while the secondary moult proceeds in centripetal order, as shown by this male Antillean Crested Hummingbird. This familiar sequence is reversed for the last two primaries in a unique but necessary inversion that helps maintain stability in hovering flight. Rectrix renewal also differs from most birds in that the outer tail feathers are moulted in advance of inner ones. Body moult commences with the shedding of primaries and continues until their replacement is completed. The moult of iridescent feathers, however, tends to take place last of all, often several weeks after the primaries have been fully renewed; this presumably ensures that plumage important for signals is in the best possible condition for the breeding season.

[*Orthorhyncus cristatus exilis*,
Le Lamentin, Martinique.
Photo: R. Tyrrell]





Different species of hummingbird occupy widely divergent ecological niches, especially in the tropics where specialization is promoted by high resource levels and intense competition. Temperate species, such as the Green-backed Firecrown, compete in species-poor hummingbird communities in search of scarcer resources, a system which favours generalism. Partly for this reason, the species can be found in a wide variety of habitats including forests, deserts, mountains and open country. It visits southern Patagonia and Tierra del Fuego in the local summer, migrating northward to northern Chile and Argentina during the winter.

[*Sephanoides sephanioides*, Los Alerces National Park, southern Chile. Photo: Günter Ziesler]

mobbing noises. Threat behaviour by flight attacks is exhibited especially by female hummingbirds against intruders near their nesting sites, even if they are not potential predators.

Some typical habits are known for closely related groups, indicating that specific forms of behaviour may be of importance for the reconstruction of phylogenetic traits. All hermits (Phaethornithinae) exhibit constant tail-wagging behaviour when perching, and the courtship of all species studied so far features fanned rectrices and wide-open bills displaying the yellow, orange or red interior base of the lower mandible in the Gape Display. These habits are not known for any of the non-hermit species. In the Andean trochiline assemblage (*Chalcostigma*, *Metallura*, *Eriocnemis*, *Haplophadja*, *Urostroke*, *Oreocnemis*, *Aglaiocnemis*, *Boissonneaua* and others) a typical habit is to keep the wings stretched out for a second or so after landing on a perch.

General habits, and their associated behavioural background, are poorly studied in trochilids. The same is true of hummingbird vocalizations and song-learning capacities, research fields which could lead to a holistic approach to understanding the evolution of life-history traits in one of the most species-rich Neotropical avian families.

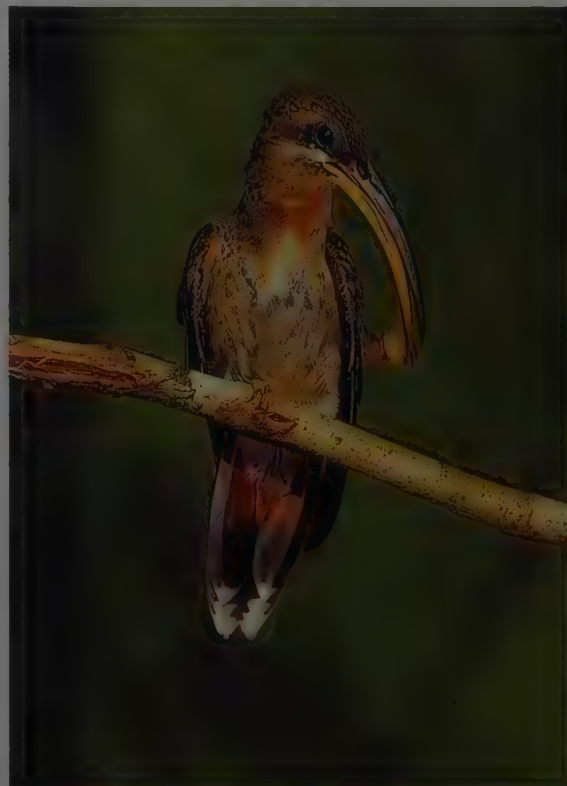
Voice

In their usually cluttered habitats, hummingbirds are often heard before they are seen. Unmelodious, high-pitched monosyllabic chirps and whistles are normally the sounds perceived during initial encounters with these birds. Their calls, often lasting less than half a second, are generally uttered by both males and females between feeding probes or from exposed perches in shrubs or tree tops, and indicate territorial birds occupying nectar-rich food sources. Chase calls, a series of aggressive rapid chattering sounds known from several species, are heard from individuals defending a feeding territory. These loud vocal signals, employed by either sex, are species-specific and an important feature for field identification.

Many trochilid species employ an advertising song of simple syllabic structure and short duration. It consists mostly of monosyllabic elements, comprising a very brief syllable of about one second and a slightly longer one lasting up to two seconds. This

acoustic advertising is repeated continuously for several minutes, sometimes for up to half an hour. Most of the songs known from hummingbirds are of high frequency, interrupted by guttural or shrill sounds, often rather unpleasant to the human ear.

Due to the minute size of trochilids many of their complex guttural vocalizations can be detected by the human ear only when at a very short distance from the singing bird. Certain elements, such as in the song of the Black Jacobin (*Florisuga fusca*), may



Hummingbirds often scratch the head and upper body by lifting the foot up and over the wing. In many species, for example the Hairy Hermit, the length of the bill precludes its use in preening these portions of the body and thus the claws may be employed for certain maintenance activities. This species is unique in that pair-bonds have been described wherein males defend females in their territories from the attentions of rival conspecifics.

[*Glaucis hirsuta hirsuta*, Burro Burro River, Guyana. Photo: Doug Wechsler/VIREO]

Hummingbirds spend a considerable amount of time preening, especially immediately after bathing.

Most species use their bills for arranging, oiling and cleaning their feathers, reaching as far up the body as bill length will allow. This Red-tailed Comet is preening the

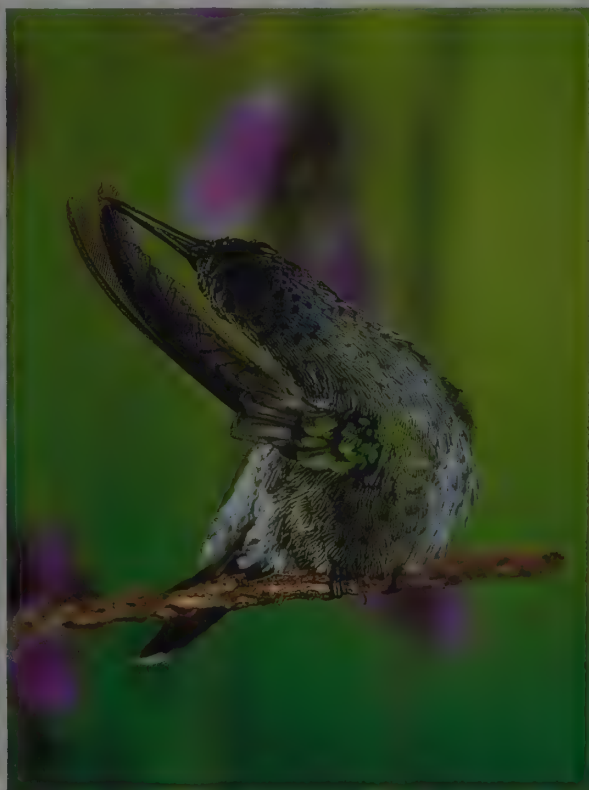
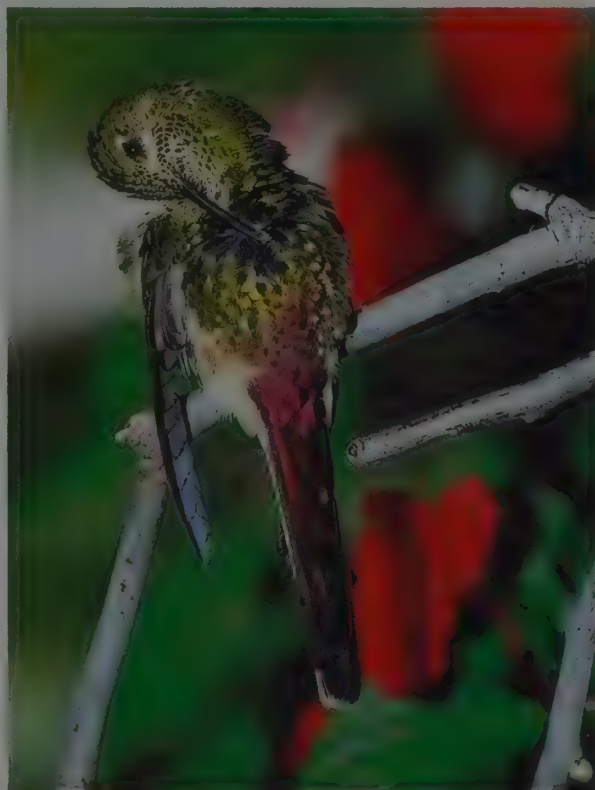
mantle feathers, or perhaps collecting oil from the oil gland. The remiges and rectrices are often arranged with the bill, as illustrated by this Violet-headed Hummingbird.

[Left: *Sappho sparganura sparganura*.

Photo: Kenneth Fink.

Right: *Klais guimeti merrittii*, Costa Rica.

Photo: Michael & Patricia Fogden]



even be completely inaudible to us, since they reach ultra-sound levels. Only rarely can certain elements of a hummingbird's vocal repertoire carry over a distance of a hundred metres. Among these few exceptions are the high whistles of the Brazilian forest-dwelling Saw-billed Hermit (*Ramphodon naevius*).

Some species employ a longer and more melodious song. The Wine-throated Hummingbird (*Atthis ellioti*) and the Vervain Hummingbird (*Mellisuga minima*) each have an elaborate musical whistle lasting over half a minute. For its attractive warbling song the Wedge-tailed Sabrewing (*Campylopterus curvipennis*) of Central America is locally called "nightingale". Among the members of the Phaethornithinae, the song of barthroats (*Threnetes*) is also known for its short warbling tunes interspersed with squeaky chirping notes. It is mainly heard during the rainy period, though often ceasing prior to the end of the wet season. Members of the hermit genus *Phaethornis*, for instance the Little Hermit (*Phaethornis longuemareus*) and the Eastern Long-tailed Hermit, perform their songs almost all year round, except during the peak of the dry season when nectar availability is drastically reduced, whereas the Blue-throated Goldentail of Central America and the Violet-headed Hummingbird (*Klais guimeti*), members of the Trochilinae, can be heard only during the dry season, falling silent at the onset of the wet period. The Rufous-tailed Hummingbird sings mainly during the short time span from dawn to sunrise.

Some hermit species of the genus *Phaethornis* and some trochilines, such as the violet-ears (*Colibri*), belong to the most persistent daytime singers of all hummingbirds, producing their vocal repertoire tirelessly from early morning to sundown. They are only silent during the months of body moult, when singing ceases in most of the hummingbird species studied.

Male Sparkling Violet-ears devote up to 70% of their daily activity to the song display. This time- and energy-demanding behaviour may have led to a loose co-operation between some conspecific male neighbours. Individuals can then perform activities other than singing, such as preening, sun-bathing or feeding, while resting assured that the singing activity is maintained. Females receptive to copulation can thus easily locate mates at almost any time of the day. Singing activity is generally associated with reproduction and is thus, as in many other birds, a reliable indication of the nesting period of each species.

Several taxa from both hummingbird subfamilies establish singing assemblies at traditional mating sites, the so-called leks. These leks may comprise two or three, sometimes up to ten, and rarely, as in the Green Hermit on Trinidad, over 20 singing conspecific males. At these advertising sites, males occupy song perches from near the ground, as in the Little Hermit, to the subcanopy level, as in the Great-billed Hermit (*Phaethornis malaris*). Females visit singing males at these leks. It would seem that the rate of singing is important in female mate choice, since males spontaneously increase their own song rate when females enter a lek site. As in other lekking birds, trochilid leks are normally of small neighbourhood size and somewhat dispersed. Since large assemblies do rarely occur, it has been suggested that a threshold of neighbourhood size decreases the probability of song interference. Furthermore, in larger groups some males would become central rather than edge birds, with less opportunity to copulate with females, which often mate with the first male they encounter. Copulation can take place on song perches or nearby.

Besides the squeaky, high-pitched persistent advertising songs performed by many lekking males (*Phaethornis*, *Amazilia*, *Polyerata*), a low-volume warbling subsong of fledglings and adults of both sexes is typical for many trochilid species. Very often aerial displays are accompanied by a specific vocal repertoire and by mechanical sounds, such as tail-feather and wing noises in *Selasphorus*, that are not employed at other times.

Vocal duetting has been reported in only one species, the Hairy Hermit (*Glaucis hirsuta*), where the female continues the whistling notes of the male with an answering guttural phrase. L. F. Baptista and K. L. Schuchmann documented song-sharing between neighbours in the North American Anna's Hummingbird, and demonstrated by experiments that song parameters such as syllabic structure, rhythm, frequency-repetition index, and syntax are the result of acquisition by vocal mimicry in this species.

Anna's Hummingbirds on Guadalupe Island, off western Mexico, produce songs distinctly different from those in mainland California. A hybrid male Anna's x Allen Hummingbird (*Selasphorus sasin*) sang an aberrant abbreviated song. In the following year the hybrid's territory was occupied by a male Anna's Hummingbird that sang a song similar to that of the hybrid. It was suggested by S. Wells and L. F. Baptista that the



Hummingbirds bathe several times a day. They often perform this ritual by sitting in shallow water and splashing about like many other bird species, but they will also perch adjacent to splashing water, and, like this Green Violet-ear, flap the wings and ruffle the feathers in the spray. In addition, hermits and some trochilines bathe by hovering just above calm water and plunge-diving briefly to wet their plumage. During rain, individual hummingbirds can occasionally be seen perching on exposed twigs spreading and vibrating the wings and tail to clean themselves. This species has the fastest registered flight of any hummingbird recorded, or for almost any other bird for that matter, with short chase flights apparently being clocked in at 150 km/hour.

[*Colibri thalassinus thalassinus*.
Photo: Stephen Dalton/
NHPA]

Anna's Hummingbird had acquired the hybrid's aberrant song through imitation learning.

The majority of songbirds, parrots and hummingbirds have in common a syrinx structure controlled by internal and external muscles. Thus it has been suggested that trochilids are capable of song learning. Support for this assumption came from A. F. Skutch who observed a Blue-chested Hummingbird (*Polyerata amabilis*) singing the song of a Rufous-tailed Hummingbird. Other indirect evidence of song learning came from observations of song-sharing by neighbouring hummingbirds in Green and Little Hermits. Recently S. L. L. Gaunt and co-workers demonstrated that the male advertising song of an Ecuadorian population of the Sparkling Violet-ear, and of populations in Costa Rica of the Green Violet-ear, are of the same song type, while the advertising songs of conspecifics from distant neighbourhoods are different. These new bioacoustical data suggest that geographical variation in song is due to cultural drift acquired through song learning.

Learning a neighbour's song could have a distinct advantage. If a neighbour's song matches the stored image of one's own song, then an undegraded image of the neighbour's song is obtained. E. S. Morton has suggested that males can use such an image as a "standard" to judge degradation of the neighbour's song over distance. By doing so an individual could assess the distance to a singing neighbour and judge whether to ignore or to threaten him by countersinging or attacking. Interestingly, playback experiments with Great Tits (*Parus major*) support this hypothesis.

Hummingbird nestlings raised in exposed cup-shaped nests do not produce begging calls; their gaping behaviour is released by specific tactile stimuli of the female prior to feeding. In contrast, nestlings raised in semi-domed or completely domed nests (*Metallura*, *Agelaiocercus*) produce begging calls 4-6 days after hatching. Obviously these behavioural differences are adaptations to reduce predation on exposed nest-sites (see Breeding).

Contact calls between young and their mothers are only heard after the fledging of the chicks. These loud and often far-carrying calls of continuous high frequency between offspring and adult females help to localize the perching position of the mostly stationary fledglings in dense protective vegetation such as tree tops. As soon as the mother gets closer to the chick, the contact

calls are answered with increasing frequency, turning into loud begging calls when the female is in sight.

Alarm calls, similar to contact calls, but very shrill and uttered at higher frequency, are known from fledglings and adults of both sexes. These vocal signals are heard when predators like snakes, raptors or other large birds have been detected near a feeding-, lek-, or nest-site. Often alarm calls are associated with flight attacks.

The study of hummingbird voice is still in its infancy. Important questions to be addressed will probably concentrate on aspects of vocal acquisition over time, such as whether learning capacities are restricted to a sensitive phase during early development stages (classical approach), or to a circannual time window during which individuals are receptive to new acoustic input independent of age (flexible learning approach). Vocalizations related to food exploitation, territoriality, and other behaviour are other eco-ethological subjects poorly understood. Furthermore, shared notes, song delivery, and vocal learning may be helpful instruments in evaluating common ancestry in some species.

Food and Feeding

Thousands of New World plant species rely exclusively upon hummingbirds for pollination. As a consequence of the year-round high energy requirements of trochilids, plants that are pollinated by hummingbirds provide nectar at all times of the year, creating the opportunity of a phenological displacement of flowering times as a means of reducing interspecific pollen flow.

The evolutionary relationship between hummingbirds and their food plants is a good example of close mutualism, resulting in the many adaptations between flower and pollen vector that together is called ornithophily. Plants that have converged upon the "hummingbird" syndrome bear relatively large flowers, solitary or loosely clustered, often placed in a horizontal or pendent position. Typical hummingbird plants open their blossoms during the day; the flowers are generally brightly coloured, often red, orange or yellow, sometimes in combination with contrasting white corolla parts. Exceptions can be found in the Gesneriaceae, where some epiphytic species ex-

A male Green-backed Firecrown takes flight after bathing in the shallow water of a stream, while the accompanying female splashes her wings to dampen her plumage. The male of this species has an iridescent crown and weighs slightly less than the female, but otherwise the sexes are relatively similar. This is perhaps as a result of reduced polygamy in comparison with many other trochilines, but so little information has been gathered about hummingbird mating systems and life-history strategies that it is impossible to do more than speculate.

[*Sephanoides sephaniodes*, Chile.
Photo: Günter Ziesler]





Adult hummingbirds are too small, aerial and skillful in flight to have many major predators. They are usually out of the reach of terrestrial carnivores, and are excessively manoeuvrable in relation to most raptors. Forest-falcons (*Micrastur*) and pygmy-owls *Glaucidium* may take a small proportion of individuals at regular lekking or feeding sites, although this has never been reported. Amongst the most remarkable of hummingbird predators is the eyelash palm pit-viper (*Bothrops schlegelii*) of Central America. It has developed the trick of waiting patiently on forest flowers until they are visited by nectarivores, in this case the Rufous-tailed Hummingbird. When the unsuspecting visitor strays within range, the snake uncoils to strike, though not always with success. Despite these dangers, the largest toll is probably inflicted by birds, such as jays (*Corvidae*) and toucans (*Ramphastidae*), arboreal reptiles and possibly bats that devour eggs or nestlings. Although direct evidence for this type of predation derives from very few anecdotal accounts, a high proportion of hummingbird breeding attempts fail inexplicably, and it is likely that nest-robbers are frequently the culprits.

[*Amazilia tzacatl* *tzacatl*, Costa Rica. Michael Fogden/DRK]



Small endothermic organisms are under severe pressure, both to meet their daily energy requirements, and to accumulate sufficient energy reserves to survive periods of low temperature and darkness.

An abundance of high-quality food is thus vital, as are mechanisms to reduce energy consumption, such as torpor. This process, enacted here by a Bee Hummingbird, is apparently a common energy-controlling mechanism in hummingbirds, involving an 80-90% reduction in metabolic rate and savings of up to 60% of the energy used in the nocturnal resting phase.

[*Mellisuga helenae*,
Playa Larga,
Zapata Swamp, Cuba.
Photo: Robert Tyrrell]



hibit solitary inconspicuous whitish flowers. However, hummingbirds are attracted to these well-camouflaged flowers by their ornamental red-edged or red-centred leaves, a little-studied advertisement strategy in hummingbird-pollinated plants known as phyto-flagging.

Some of the commoner hummingbird-pollinated species belong to the genera *Zauschneria* (Onagraceae), *Delphinium* and *Aquilegia* (Ranunculaceae), *Mimulus* (Scrophulariaceae), *Aphelandra* (Acanthaceae), *Centropogon* (Lobeliaceae), *Cavendishia* (Ericaceae), *Columnnea* (Gesneriaceae), *Psittacanthus* (Loranthaceae) and *Heliconia* (Heliconiaceae). Most ornithophilous plants are dicotyledonous perennial herbs and shrubs, and only a few trees are pollinated by hummingbirds. Flowering trees with a very large nectar source, like many *Erythrina* (Leguminosae) species, are quickly occupied by territorial hummingbirds which remain in the tree tops for the whole flowering period until the nectar declines. By their doing so, pollen flow is greatly reduced. The most efficient pollinators of ornithophilous trees in America are passerines, such as orioles (*Icterus*), which move in groups between widely scattered flowering trees. The pollen loads from different conspecific trees, deposited on their feathers, support the obligate reproductive system of these trees: cross-pollination.

A closer examination of the mutualistic relationship between hummingbirds and their food plants has shown that pairwise co-evolution between a certain trochilid species and a certain plant species is non-existent. Plant-bird mutualisms are best described as having originated by "diffuse co-evolution", in which hummingbird-pollinated plants and their pollinators are represented by an array of populations generating multiple selective pressures.

K. A. Grant and V. Grant hypothesized that most of the Nearctic hummingbird-pollinated plants stem from bee-pollinated blue-flowering ancestors, and to a lesser extent from butterfly or moth pollination systems. An adaptive shift from blue to red flowers, which are not attractive to most insects (except butterflies and beetles), may have led to the evolution of ornithophilous flowers. This scenario may also be true for many Neotropical plant species. Most of their temperate relatives originated in tropical environments and followed the hummingbirds in the course of their various radiations.

The corolla of a typical hummingbird flower is often long, thickened, tubular in shape, and scentless. It contains sucrose-rich nectar which is taken by trochilids in hovering or hover-clasping flight. Many characteristics of hummingbird-pollinated

flowers, such as red colour, lack of odour, or the floral tubes with their thick walls, are adaptations either to avoid attracting insect competitors or to prevent nectar robbing. Ornithophily seems to be energetically expensive for plants. Although the energetic expenditures of plant reproductive strategies are still poorly understood, it is most likely that this process is energy-demanding. The evolution of ornithophily must therefore be viewed from the perspective of costs and benefits, obviously well balanced between hummingbirds and their plants.

Vision is the main sensory cue for foraging hummingbirds. Their colour vision is highly sensitive towards the red end of the spectrum (long wavelengths), whereas most insect colour vision is optimal at short wavelengths. The majority of ornithophilous flowers employ long-wavelength colours, reducing their attractiveness to most insects. Hummingbirds, according to current knowledge, have no sense of smell, but may well differentiate nectar by taste and concentration. However, they have no innate preference for red flowers, but instead associate particular colours with nectar content. Experiments by F. G. Stiles revealed that hummingbirds responded more to a stronger nectar concentration and nectar flow than to sugar composition (taste), and responded least to colour of food source, whether feeder or flower.

Since nectar is the major reward for hummingbirds when serving as pollen vectors, ornithophily has been examined mainly from the point of view of energetics. It has been proposed that feeding success depends on: the cost of acquisition, which is determined by body size; the energy value, which is influenced by co-evolutionary factors; and the time periods over which net energy benefits are obtained. If the absolute nectar accumulation rate were limited only by crop volumes and crop emptying rates, then trochilids could satisfy their theoretical energy needs during a short period of intensive daily foraging. Why is this not the case?

F. R. Hainsworth experimentally addressed the question of why hummingbirds adjust energy storage via meal size but maintenance via feeding frequency. According to his model, the answer depends on the weight of a meal as a cost. A meal of a particular size makes a particular contribution to the maximization of the rate of net energy gain, within constraints imposed by the total energy expenditure of the previous night. Meals of variable sizes have variable costs depending on their weight, and this uncertain variation may not permit a maximization of this rate. If hummingbird foraging strategy is looked at on a daily time scale, then short-term feeding behaviour may be sensitive to energy use for longer-term storage as well as short-term maintenance.



Hummingbirds are belligerent in defence of their territories or resources. Males often use exposed perches, which serve as vantage points whence interlopers can be detected. In this event threat calls are often given in conjunction with agonistic flights. If the newcomer does not vacate the territory, contests rapidly escalate, quickly culminating in physical combat. Individuals will sometimes grasp each other in flight, such that they tumble to the ground. While the claws are often the weapons used, the bill too is employed in attack, as seen in these two Ruby-throated Hummingbirds contesting the possession of a perch. Hummingbird fights can appear surprisingly vicious, but they are rarely harmful beyond the loss of a few feathers.

[*Archilochus colubris*,
Sodus Bay,
New York, USA.
Photo: Robert Tyrrell]

Seasonal changes in day length, as in North America and southern South America, can also influence the apportioning of energy to maintenance and storage, while energy-demanding activities like reproduction, moult or migration will also influence feeding behaviour. Depending on demand for and availability of food, short-term adjustments in daily rates of net energy gain may suffice for some seasonal effects such as daylight variation. If foraging time is limited (migration), or if expenditure is increased relative to food availability (reproduction), then longer-

term accumulation of energy might be required in "anticipation" of demand.

Hummingbird flowers supply their pollinators with large amounts of nectar per flower per day, but do not satisfy their nutritional requirements at one visit. However, P. Feinsinger discovered in a Costa Rican heliconia (*Heliconia psittacorum*) that only some flowers contain abundant nectar (bonanzas), and some essentially none (blanks). Since hermits are the main pollinators of heliconias, Feinsinger suggested that these hummingbirds must

visit many flowers in order to encounter one with a high nectar content, thus the "bonanza-blank pattern" might support cross-pollination in *H. psittacorum*. In another field study on the pollination of successional plant species in the cloudforest at Monteverde, Costa Rica, Feinsinger observed that flowering was staggered among plant species, resulting in a constant nectar supply to trochilids. In five plant species that were closely investigated, measurements of nectar volume indicated that the bonanza-blank pattern was widespread. He concluded that plants may conserve energy by producing large numbers of nectarless flowers and a few bonanza flowers so that hummingbirds are forced to visit many flowers to meet their energetic needs. By their visiting many flowers, cross-pollination is promoted.

Many studies show a significant correlation between the body mass of hummingbirds and the energy value of the nectar produced per flower and day. Hummingbirds have a greater body mass than most insects, and this, combined with endothermy, increases their energy requirements, necessarily leading to increased mobility. This considerable activity radius increases the probability of cross-pollination and the genetic recombination of flowering plants. Only a few species of large hawkmoths have higher energetic needs when active than hummingbirds but, in common with other insects, reduce their metabolism when weather conditions are unfavourable. Hummingbirds use nocturnal torpor for short-term energy savings, remaining active even under inclement conditions during the day when insects are inactive, and are thus more reliable pollinators where cool or rainy conditions occur regularly. Hummingbirds, like other nectarivorous birds, forage throughout the day, with higher levels of activity at dawn and dusk, although only a small fraction

of each hour may actually be spent feeding. Insects search for nectar only at certain periods of the day. Due to their relatively high body mass hummingbirds have a much higher potential mobility than most insects. Foraging distances of more than 1 km have been reported for trochilids visiting widely distributed flowering shrubs in a single feeding bout. For most insects the travelling distance between successive flower visits tends to be much smaller and foraging strategies are much more stereotypic. A long-lived pollinator such as a hummingbird, experiencing several flowering seasons during its lifespan, combined with the capacity of its excellent spatial memory, can easily remember locally or patchily distributed flower stands. Thus, the floral environment for trochilids is much more differentiated in time and space than for insects.

The most striking feature when considering hummingbirds and their flowers is the close fit between their bill shape and length and the flowers on which they feed. Like the insect feeding apparatus, bills are evolutionarily plastic structures. Selective forces have had a much stronger impact on morphological co-adaptations between bird bills and flower shapes than between the snout structures of bats and bat-pollinated flowers. This may generally explain the higher species diversity of flower-visiting birds and insects as compared to bats.

Bill morphology influences the efficiency with which hummingbirds forage at each flower and determines which flower types can be exploited. P. Feinsinger and R. K. Colwell suggested five major flower types, often sympatric within a tropical floral community, according to habitat, zone within a habitat, dispersion, and flower characters. The five types are: (1) "Dispersed rich flowers" with long or curved corollas that exclude most in-

Flowers are the main source of food for hummingbirds, and for thousands of New World plants, hummingbirds are the key to reproduction.

Because of this interdependency, selective processes driven by competition for resources and pollinators have shaped these organisms, producing a fantastic array of colour and form.

The Blue-fronted Lancebill, here visiting a vivid inflorescence of nectar-bearing flowers, is a member of the genus *Doryfera*, which was previously grouped with hermits because of the similar musculature and vocalizations. This genus has subsequently been regrouped in the heterogeneous trochiline assemblage, of which it is potentially an early evolutionary state, and merely convergent with hermits in behavioural and morphological traits, as they are adaptations for foraging, communication and locomotion in the dense forest understorey.

[*Doryfera johannae*
johannae,
Mocoa, Putumayo,
Colombia.

Photo: Luis Mazariegos]





The Bronzy Inca, here attending banana blossom, often begins feeding well before dawn, so urgent is its year-round requirement for nectar. As a consequence of this demand, plants with flowers designed to attract hummingbirds often provide nectar constantly, unlike the seasonal production found in insect-pollinated plants. Hummingbirds consume a surprisingly large amount of insect food, usually in the ratio 1:9 with nectar. It was previously suggested that hermits tend to rely on a greater proportion of insects than do trochilines, but investigations have not supported this idea. Small quantities of vegetable matter are also taken by many species.

[*Coeligena coeligena ferruginea*, Cauca, Colombia. Photo: Luis Mazariegos]

sects and most hummingbirds with short to medium-sized bills; their nectar reward is substantial. Typical plant species of this type are often vines (*Mandevilla hirsuta*, Apocynaceae) or shrubs (*Centropogon*, Lobeliaceae). (2) "Clumped rich flowers" with long corollas and high nectar production, often occurring in dense clumps; heliconias are a prime example. (3) "Dispersed moderate flowers" with moderately long corollas, excluding many insects but allowing most trochilids to exploit a moderate amount of nectar. Examples are shrubs like *Hamelia* (Rubiaceae) and vines (*Tropaeolum*, Tropaeolaceae). (4) "Clumped moderate flowers" with small to medium-sized corollas and little nectar reward, available especially in the late afternoon. These flowers exist in dense clumps on trees or shrubs, for instance some lobelias. (5) "Insect flowers" with short corollas containing minimal amounts of nectar, for example *Lantana*, *Stachytarpheta* (Verbenaceae) and *Asclepias* (Asclepiadaceae); they are often pollinated by insects.

Bill shape, which varies widely among trochilids, largely influences the efficiency with which the birds forage at each flower and determine the type they can successfully exploit. Hermits and certain trochiline species have long and straight or long and slightly decurved bills providing access to long-tubed flowers, rich in nectar. At the other extreme, many trochilines have short, straight bills allowing them to exploit a variety of "moderate" or "insect" flowers opportunistically. However, some short-billed species, like *Heliothryx*, are nectar robbers, taking nectar from flowers by piercing the corolla base.

Questions of wing-loading, the ratio between body mass and the area of the outstretched wings, and the energy required for hovering have also been used in the interpretation of hummingbird foraging modes. This energy depends on body mass and

wing-loading, which varies with air density. Hummingbirds with high wing-loading expend more energy while hovering, especially at higher elevations, but have greater flight acceleration and manoeuvrability than those with low wing-loading. Birds with high power requirements establish territories around clumped flowers, while those with low requirements exploit dispersed or insect flowers with relative efficiency.

In more complex tropical environments, hummingbird communities may be grouped into different foraging modes according to the power required. "High-reward trap-liners" with specialized long bills (almost all of the hermits and some non-hermits) visit widely scattered long-tubed, nectar-rich flowers following a repeated foraging circuit, or trap-line. "Low-reward trap-liners" have smaller straight bills and visit dispersed but less specialized flowers. "Territorialists" occupy "clumped moderate" and "clumped rich flowers". These are generally small hummingbirds with short bills and a moderate to high power requirement, and they defend feeding territories against any potential hummingbird intruder. "Territory-parasites" frequently occur in "clumped moderate" flowering stands, parasitizing the territory holder. These parasitizing trochilids may be large with medium-sized bills and high power output, and tend to ignore aggressive displacement displays by the territorial bird, or they may be very small like *Lophornis* and *Atthis*, resembling large insects, and feed at areas within a territory not directly visible or regularly inspected by the resident bird. "Generalists" have short to medium-length bills, small to medium body mass, and a moderate power requirement. They behave opportunistically, switching from dispersed moderate to clumped flowers. These generalists are often called "facultative trap-liners" since they

Many species of hummingbird visit Heliconia flowers, often as bizarre and beautiful as the birds themselves. Indeed,

White-bearded Hermits and other Phaethornithinae are the primary pollinators of these pendant candelabra-like structures which commonly festoon the undergrowth of Neotropical forests. Heliconia has been found to follow a "bonanza-blank pattern", in which some flowers are rich in nectar and others contain very little. By this method, they are thought to reduce energetic costs and increase the probability of cross-pollination, as hermits have to visit more flowers to meet their nutritional requirements. Sitting quietly by a clump of flowering Heliconia, an observer might notice that it is visited by an individual hermit at regular intervals. The reason for this is that hermits are "high-reward trap-liners", visiting a sequence of widely dispersed nectar-rich flowers in a repeated circuit. The advantage of this technique is that each flower is given sufficient time to renew its nectar resource. Between trap-lining and territoriality, many intermediate forms of resource defence and exploitation are found in hummingbirds, depending on flower dispersion, morphology and nectar reward. The behaviour of individuals or populations can vary spatially and seasonally, depending on these parameters. In addition, hermits often pick both spiders and their prey from webs, or insects from vegetation. They rarely hawk for flying insects, although this is a common foraging technique employed by many trochilines.

[*Phaethornis hispidus*,
Tambopata Reserve,
Peru.

Photo: Günter Ziesler]





may switch to low-reward trap-lining depending on the local nectar availability and competition for food.

In Central America, where the dynamics of local hummingbird communities are seasonally influenced by North American migrants, different foraging guilds can be found. In a Mexican hummingbird community, J. L. Des Granges distinguished three well-defined foraging guilds: a resident guild of tropical species, inhabiting specific habitats; a guild moving through several habitats following seasonal flowering periods (wanderers); and a guild of strictly seasonal migrants. According to this study most residents could be viewed as territorial species, whereas the wanderers could be categorized as trap-

liners, being mainly non-territorial. Like the residents, the migrants established territories and defended flowers that provided nectar surplus to the energetic needs of residents and wanderers. Des Granges also noted spatial segregation of species utilizing flowers at different heights.

When hummingbirds visit their food plants "nectar mites" feeding inside the flower on nectar and pollen often make use of the avian visitor for a change of blossom. Within a few seconds they climb to the bird's bill and move to the nasal cavities, where they remain until the bird visits another host plant. The mites do no harm to the bird. They undergo their complete reproductive cycle in hummingbird flowers, which they identify as host plants by odour. They complete the stages from egg to adolescence within four to seven days, then wait for another hummingbird to move them to new host flowers for another reproductive cycle.

Hummingbirds in North America and Colombia have been observed making use of sapsucker (*Sphyrapicus*) pits in living trees, consuming the sugary sap and catching insects attracted to this food source. The Ruby-throated Hummingbird of North America, in particular, seems to benefit from these sugar sources during early spring migration when plants are just beginning to flower. Other trochilids (*Leucochloris*, *Chlorostilbon*) in Santa Catarina, Brazil, have been recorded feeding on the sugar-containing excrement of coccids (scale insects) during the southern winter when flowers are scarce.

Hummingbirds often supplement their usual food with pollen gathered when drinking nectar. Although pollen contains essential amino acids, the major protein supplement comes from arthropods. It has often been stated that hermits differ from trochilines by their higher insect consumption, but this idea has not been confirmed by laboratory or field studies. F. G. Stiles, for example, concluded from his detailed work in Costa Rica that there is no support for the view considering hermits to be more insectivorous than trochilines. As a general approximation, most hummingbirds consume a daily ratio of nectar to arthropods of roughly 9:1 by mass.

Hermits, which exclusively live in the understorey, are hover-gleaners, collecting their arthropod prey from the plant substrate or spiders' webs. The Band-tailed Barbthroat (*Threnetes ruckeri*) forages for jumping spiders; the White-tipped Sickbill

The Oasis Hummingbird lives in relatively inhospitable habitats of the Peruvian and Chilean deserts, occurring in dry coastal hills, arid scrub and oases, where cactus flowers are an important source of nourishment. It is also quick to take advantage wherever man has increased the local abundance of flowering plants by frequenting towns and gardens.

[*Rhodopis vesper vesper*, Apurímac, Peru.
Photo: Günter Ziesler]



*A remarkably diverse hummingbird community flourishes at relatively high altitudes in páramo habitats. The Shining Sunbeam, for example, feeds on flowering terrestrial bromeliads and composite shrubs in these areas, often competing with hillstars (*Oreotrochilus*), trainbearers (*Lesbia*) and thornbills (*Ramphomicron*, *Chalcostigma*). As flowers of páramo plants are generally numerous but small, the bills of attendant hummingbirds tend to be rather short.*

[*Aglaeactis cupripennis cupripennis*, El Angel Reserve, Ecuador.
Photo: Günter Ziesler/
Bruce Coleman]

Typical hummingbird flowers contain sucrose-rich nectar, open diurnally and tend to be large, brightly coloured and eye-catching, with long, tubular and scentless corollas. Red colours predominate because of the spectral sensitivity of hummingbird eyes. Some dull-coloured flowers are surrounded by colourful leaves so that they are conspicuous to nectarivores, a phenomenon known as phyto-flagging. While some flowers are favoured by particular species of hummingbird others attract a variety. This epiphytic bromeliad is visited by a Violet Sabrewing and a Green-crowned Brilliant, and in some areas popular flowers will attract more than ten species in a day. In species-rich hummingbird communities, sympatric taxa often differ widely in body mass and bill morphology, as natural selection tends to minimize direct competition. When species are more similar in morphological respects they often diverge ecologically by employing different foraging strategies or microhabitat preferences. Hummingbird foraging behaviour is exploited by "nectar mites" that feed inside flowers and use birds as their mode of transport, crawling on to their bills, sheltering in their nasal cavities and hitching a ride to the next plant.

[Above: *Campylopterus hemileucurus mellitus*, Costa Rica.

Below: *Heliodoxa jacula henryi*, Costa Rica.

Photos: Michael & Patricia Fogden/BBC Natural History Unit]





The Broad-tailed Hummingbird usually feeds just above the ground on insects and the nectar of flowering shrubs and low perennials. This bird has been startled while feeding on the beard tongue (*Penstemon barbatus*), and in its haste to escape danger small beads of nectar spray from its bill. Its modified wingtips, featuring reduced outer primaries, are thought to function in mechanical noise production, as a wing-snapping sound is regularly heard from males.

[*Selasphorus platycercus*, Mt Lemmon, Arizona, USA. Photo: Robert Tyrrell]

(*Eutoxeres aquila*) seems to be an exception among the hermits with its habit of hawking for flying insects.

In most trochilines such hawking is a common foraging mode. Flies and wasps are the dominant prey, but spiders, ants and small beetles have also been found in the stomachs of non-hermits. Both *Heliothryx* species are hover-gleaners, making use of the complete vertical stratum of the tropical vegetation from close to the ground right up to the canopy; according to F. G. Stiles they take more spiders than flies. A spider specialist among the trochilines is the Tooth-billed Hummingbird (*Androdon aequatorialis*), which probes for prey in rolled-up leaves or cavities along roadsides, where hunting spiders often hide.

Observations that hummingbirds can rely over extended periods on arthropods alone must be viewed with some scepticism, as does a report that arthropod abundance and not nectar availability determines the onset of breeding in dry areas. Nectar seems to be the only energy source that could supply the daily requirements of a high-metabolism animal like a hummingbird. It has been reported that breeding female hummingbirds spend more time foraging for arthropods than do males at the same time in the same localities, but foraging for nectar still accounts for most of the daily activity pattern.

There is no evidence that hummingbirds can extract arthropods from flowers with the bill or tongue. It is more likely that selection for nectar drinking was the major evolutionary force in the development of the hummingbird feeding apparatus, so that bill morphologies in turn constrain foraging methods to gleaning and hawking when feeding on arthropods.

Breeding

Male hummingbirds are polygynous, mating with several females during a reproductive period. In most species studied the male associates with the female only during a short period to fertilize her eggs. All remaining reproductive responsibilities like nest building, incubation, and rearing the young are carried out solely by the female. There are a few reports, involving the Sparkling Violet-ear and the Hairy Hermit, of males participating in incubation or feeding young, but recent studies of the reproductive biology of both species did not confirm parental care by males as a regular species-specific behaviour pattern. Since both species are sexually monomorphic, the male participation in incubating the eggs or rearing the young might easily have been a misinterpretation. The same is true for the White-necked Jacobin, for which observations of male incubation are said to have been made. Again, a closer look at the external morphology of the species reveals that some females may moult into a sexually distinguishing plumage only in their second year. When entering

their first reproductive cycle they may still look much like adult males. There are a few other single reports of male incubation in North American trochilids, namely Ruby-throated, Rufous and Anna's Hummingbirds, but whether these observations are random exceptions or commoner phenomena still needs verification. By no means can broad generalizations be made about active male participation in reproduction for any of the North American species solely on the basis of these observations.

Interactions between male and female hummingbirds are normally restricted to the short period of sexual synchronization. Males advertise themselves by song, iridescent plumage (Trochilinae), and aerial flights either at traditional display grounds, or leks, from dispersed singing posts, or at their feeding territories where they are visited by females when receptive to copulation. The male behaviour for attracting females is similar to the defence display directed towards food competitors, predators or any intruder to the feeding ground. By specific behavioural triggers, mainly perching motionless near an advertising male, the female switches the agonistically orientated display of the male into one which is sexually directed and leads to copulation. Thereafter, both sexes separate again. Males of the Fiery-throated Hummingbird and Purple-throated Carib, among others, show a resource-based mating system, allowing conspecific females to enter their otherwise aggressively defended territories to feed on nectar-rich flowers. Females may copulate with males on these feeding grounds or may collect nectar for themselves or their offspring during the period of reproduction. In hillstars (*Oreotrochilus*) only females hold territories, on which they are visited by males in the breeding season. For one species, the Andean Hillstar, the female has been observed to feed the male prior to mating. Loose pair-bonds with one or two brooding females have been reported for males of the Hairy Hermit along sections of small forest streams, the males protecting their mates from other hermits which approach and inspect active nests in the search of nesting material.

The onset of breeding in hummingbirds is very variable from species to species and from region to region. As a general rule the peak of reproduction in most trochilids is closely associated with the months of mass-flowering of many ornithophilous flowering plants. In the high Andes of Ecuador, violet-ears (*Colibri*), metaltails (*Metallura*), trainbearers (*Lesbia*) and pufflegs (*Eriocnemis*) begin to breed during most of the wet season, often around mid-October, and continue to March or sometimes April. At similar altitudes further north or south, reproduction starts about three months earlier or three months later than in the mountain regions near the equator, the breeding season often lasting only a few weeks. At lower altitudes, seasonality of the reproductive cycle declines and nests of several species may be found throughout the year, with decreasing numbers during the peaks of the

Hummingbird bills are evolutionarily plastic structures, and natural selection has sculpted various styles.

The Green-fronted Lancebill, for example, has an extremely long, straight bill for extracting nectar from tubular corollas, such as this *Psammisia ramiflora* flower, but it cannot probe into curved flowers. The Green Hermit has a slightly decurved bill, allowing it to feed in a wider variety of plants, including these *Erythrina* flowers, while the White-tipped Sicklebill specializes on curved flowers like those of *Heliconia reticulata* but cannot utilize long, straight corollas.

The Scintillant Hummingbird has a short bill, ideal for small flowers, such as *Vaccinium poasanum*. Close mutualism between hummingbirds and flowers is termed ornithophily, a dynamic strategy with finely balanced costs and benefits for both parties.

There is no evidence for any exclusive inter-relationship between single species of plant and hummingbird, and mutualism is perhaps best described as "diffuse co-evolution", a process by which a suite of bird and plant populations combine to generate selective pressures, through which the shapes of flowers and hummingbird bills are determined. It has been hypothesized that insect-pollinated ancestors of ornithophilous plants switched from blue to red colours as a result of differences in the optical design of their pollinators: the compound eyes of insects are sensitive to blue light while those of hummingbirds are most sensitive to red light.

[Above left: *Doryfera ludovicae veraguensis*, Costa Rica.
Above right: *Phaethornis guy coruscus*, Costa Rica.
Photos: Michael Fogden/DRK.

Below left: *Eutoxeres aquila salvini*, Costa Rica.
Below right: *Selasphorus scintilla*, Costa Rica.
Photos: Michael & Patricia Fogden]





dry and wet seasons; these seasons differ greatly from region to region. The Hairy Hermit on Trinidad and Tobago breeds mainly during the dry season, from January to April, with declining reproductive activities from the onset of the wet period in May. In the Amazon region of Brazil the same species also nests during the dry months, which there last from May to October. The Rufous-tailed Hummingbird, a species which occurs from central Mexico to western Venezuela and western Ecuador, breeds virtually throughout the year, except during its annual moult, with locally different peaks of reproduction. The same applies for the cave-nesting hillstars of the high Andes. North American trochilids (*Selasphorus*, *Archilochus*, Costa's Hummingbird, *Calothorax*, *Stellula*, *Eugenes*, *Lampornis*) chiefly breed during

spring to late summer, with the exception of Anna's Hummingbird, which generally nests during winter; sometimes incubating females of this species are exposed to frost and snow. Its early breeding has been explained as a strategy of competition avoidance with other temperate trochilids which invade the coastal Californian scrub zone (chaparral), one of the major habitats of the species, during the flowering peak of several nectar-rich food plants, such as gooseberry and fuchsia, in spring.

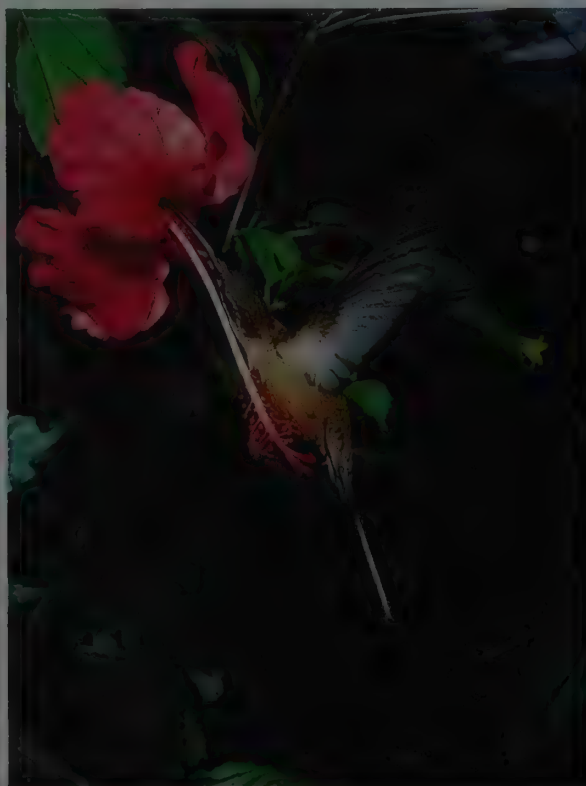
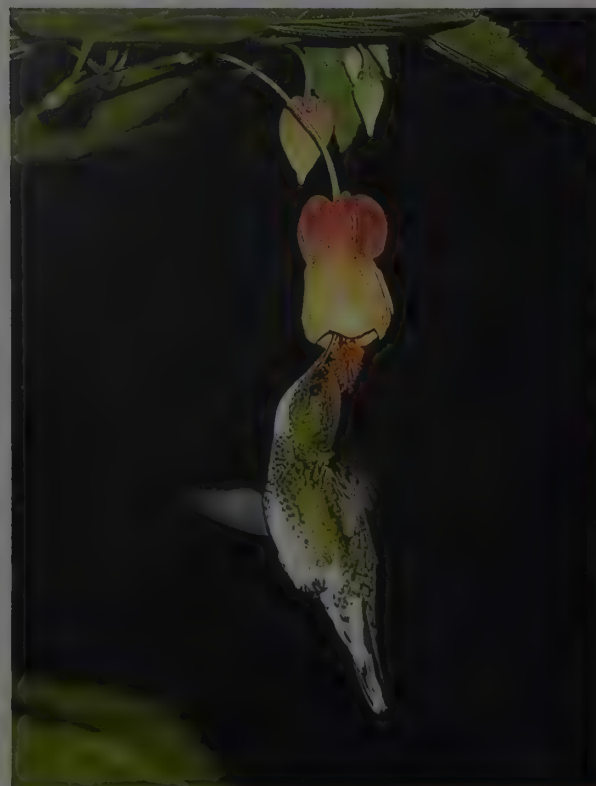
Increase in testis size as an indication of breeding condition has been studied in detail only in Anna's Hummingbird. In this species a testis volume of 4 mm³, or greater, has been taken to be an attribute of birds ready for reproduction. Broad generalizations have been made with regard to testis volume and the onset of breeding based on these findings, and it is fairly clear that a testis size of 6 mm³ is a reliable indicator of reproduction in many medium-sized hummingbirds throughout their distribution range. However, reproductive physiology in the great majority of trochilids remains unstudied. Completion of moult may be a general prerequisite for breeding.

Females of many Trochilinae select nest-sites after a nearby rich nectar source has been located. Suitable branches for nesting are first inspected by her hovering above the surface and touching down over the spot repeatedly. Nest-sites of hermits, however, are not associated with nearby food sources. Females of this subfamily frequently cling with their feet to suitable green leaves of palms or *Heliconia* stands, to which they later attach their cone-shaped nests. This behaviour may serve to test the strength of the stratum for the purpose of nest construction.

Hummingbird nests are tiny and of various shapes, and they are placed at a wide range of heights, locations and substrates. Most nests are of a cup-like architecture, saddled on branches and large leaves (*Anthracothonax*, *Florisuga*); placed in forked twigs (*Thalurania*); glued to rocky walls (*Oreotrochilus*); hidden underneath a bulk of dense thickets overhanging a slope (*Eriocnemis*, *Lesbia*); attached to lianas (*Heliothryx*); or fastened beneath a pendular leaf which provides shelter from rain (*Haplophaedia*, most Phaethornithinae). Some genera like the sylphs (*Agelaiocercus*) construct completely domed nests, others like the metaltails have semi-domed ones. In sylphs, males too have been observed building "nests", but these serve only as nocturnal sleeping shelters to which they return each night.

Plants provide nectar to attract hummingbirds. During the feeding process, pollen is attached to the bird in such a way that it is transported to the next flower visited, which may thereby be fertilized. By this process of pollination, the Ruby-throated Hummingbird performs a vital ecological service. Due to a lack of food in winter, it is forced to vacate its North American breeding range. Small groups migrate directly across the Gulf of Mexico, flying up to 1000 km. The birds have been calculated to accrue sufficient fat reserves to travel 40 km per hour for 25 hours: only just enough to cross the sea!

[*Archilochus colubris*,
Sodus Bay, New York.
Photo: Robert Tyrrell]



The anthers of some flowers are designed to dab pollen on the crowns of their visitors, as illustrated by this White-throated Hummingbird, while others reach their belly plumage, as in the hibiscus here attended by an Eastern Long-tailed Hermit. In comparison with insects, hummingbirds are active for a greater part of the day, tolerate poorer weather, have superior spatial memory and live longer. They also have higher energy needs due to their endothermy and greater mass, which lead them to be more mobile in search of food, a factor which further increases the likelihood of cross-pollination.

[*Leucochloris albicollis*,
Mar de Plata, Argentina.
Photo: Yves Bilat.

Phaethornis superciliosus
superciliosus,
French Guiana.
Photo: Jany Sauvanel/
NHPA]

Some species, such as the Stripe-tailed Hummingbird, have learnt to bypass the requirement for long bills by occasionally piercing the base of flowers and thereby gaining access to the nectar. By doing so, they also bypass the plant's pollination system and thus make no contribution to its reproduction. For this reason, ornithophilous flowers often possess thick sleeves to minimize the incidence of nectar theft. The Stripe-tailed Hummingbird is locally common from Mexico southward through Central America in damp montane forests.

[*Eupherusa eximia*
egregia,
Costa Rica.
Photo: Michael &
Patricia Fogden]



Nests can be found at all heights, from a few centimetres above the ground (*Phaethornis*) to tree-top levels at 10-30 m (*Anthracothorax*, *Eulampis*, *Heliomaster*, *Eugenes*). Even within a species, nest-sites may vary from low secondary vegetation to the canopy level. Although all hummingbird nests are accessible in flight, only a few species build them completely exposed, for example members of the genera *Anthracothorax* and *Heliomaster*. Nests are commonly placed in locations giving some protection from direct sun and rain by overhanging leaves. For nest-site selection balanced microclimatic conditions like temperature and humidity seem to be major requirements for ensuring the successful development of the embryos. Thus nests are often located near waterfalls, forest streams or lake shores.

Many hummingbirds decorate the outer wall of the nest with pieces of lichen, moss, dead leaves, rootlets, bark and so on, making it almost indistinguishable from the immediate surroundings, and thus difficult for predators to locate. Most members of the Trochilinae have nests of cup-shaped open construction consisting of two different substrate layers. The outer surface often contains the coarse materials mentioned for optimal camouflage, the whole bound together with spider web into a solid mass. Soft, fine plant materials, and occasionally small feathers or animal hair, are used for the inner nest lining, providing optimal insulation during incubation. Among the exceptions are nests of high-altitude hummingbirds, like the Sapphire-vented Puffleg (*Eriocnemis luciani*), in which the inner soft cup layer is absent. Montane trochilids often build bulky nests of moss, pieces of grass and lichen held together with spider web, frequently placed underneath dense thickets of grass overgrowing steep slopes and roadbanks, which provide ideal microclimatic conditions and protection for the eggs and young.

Hermit nests are mainly attached to the inner side of a palm or *Heliconia* leaf tip, or, as in the Sooty-capped Hermit (*Phaethornis augusti*), suspended from above by a single strand of spider silk. In order to achieve a stable vertical nest position, organic matter such as fine rootlets, leaves, parts of downy pappus, and so on is attached to the lower part of the nest, which may triple the size of the actual construction. To keep the hanging position of the nest level, lumps of clay or pebbles are woven in below the point of attachment. Nests of the Sooty-capped Hermit are regularly found inside empty buildings or beneath bridges.

Members of the genus *Phaethornis* construct compact pendant nests of soft plant fibres and spiders' webs attached to the inner side of elongated plant leaves. All other hermit genera build similar but loose nests with open walls of coarse material such as stiff rootlets or dry pieces of leaves and liverworts. Generally, the eggs can be seen from below since much light passes through the construction. This nest structure is an adaptation to the wet lowland forests where most hermits occur. The regular heavy rain showers have no cooling effect on the eggs and embryonic development since water passes through the nest quickly. The poor insulation provided by the coarse nest material is largely compensated for by the warm ambient lowland temperature.

The nest construction process lasts around 5-10 days for most species studied. Building begins in the early morning and continues actively until late morning, slowing to a stop around mid-afternoon. In the Rufous-tailed Hummingbird and many North American trochilids, nest construction may continue all day, depending on local weather conditions. The female makes alternating trips between gathering plant down and spiders' webs. The sides and rim develop as the female sits in the nest, pushing nest material with her breast while turning frequently. Often nesting material is re-used in a new nest or the old nest serves as a platform for a subsequent construction: a female Blue-throated Hummingbird (*Lampornis clemenciae*) has been known to build five consecutive nests on the first one, creating a nest tower of over 20 cm. Females repair nests regularly, especially during the incubation period.

The clutch of all hummingbirds consists invariably of two eggs which are white, non-glossy, and of an elliptical oval shape. Only in the Stripe-tailed Hummingbird (*Eupherusa eximia*) of Central America have bright pinkish eggs been reported, besides the regular white clutches. This difference in egg coloration is not genetic but is caused by the red oak lichen sometimes used in the lining of the nest. Rain leads to a permanent chemical colour reaction with the eggs and the belly feathers of the incubating female, which are regularly stained with the same pinkish hue.

In some hermits (*Glaucis*, *Threnetes*), nests with three or four eggs have frequently been found, but these are apparently attributable to more than one female, so-called egg-dumping, and females of both genera regularly inspect active nests of conspecifics.

Occasionally three eggs have also been found in the nest of a few trochilines (*Colibri*, *Amazilia*, *Calypte*), and again it is most likely that the additional egg was laid by another female. Eggs are usually laid in the early morning. Normally there is an interval of two days, rarely one or three, before the second egg is laid. Eggs are sometimes laid before the nest is completed; females then continue construction between incubation spells. Incubation may begin when the first egg is laid but regular incubation starts with the second.

Hummingbird eggs are naturally very small. Eggs of the tiny Bee Hummingbird from Cuba average 11 x 8 mm, while those of the much larger Giant Hummingbird of the Andes have a size of 20 x 12 mm. Egg mass varies from 0.4 g in extremely small species, such as the Reddish Hermit and the Frilled Coquette (*Lophornis magnificus*), to 1.4 g in the Giant Hummingbird. In relative terms, however, two eggs of the small species would equal roughly 35% of female body mass, while in the Giant Hummingbird the figure is about 15%. The severe energy constraints



The bill of the Sword-billed Hummingbird, reaching 12 cm in length, is the longest of any trochilid, and the bird needs to hold it up towards the vertical when perching or in flight so as to maintain its balance. Despite this minor inconvenience, the species is perfectly adapted to extract nectar from the long tubular flowers of Andean plants such as *Datura sanguinea*. The hummingbird has evolved in tandem with flowers like this and is their most frequent visitor in many areas. To a certain degree this kind of mutualism is beneficial to both parties, guaranteeing the flower a dedicated pollinator and eliminating competition for the hummingbird. The system does, however, leave itself open to cheats, as illustrated by this Black-tailed Trainbearer, piercing the *Datura* flower at its base, taking the nectar supplies coveted by the Sword-billed Hummingbird and failing to pollinate the plant.

[Above: *Ensifera ensifera*, Ecuador.

Below: *Lesbia victoriae victoriae*, Ecuador.

Photos: Günter Ziesler]



As they process such large quantities of liquid food, hummingbirds defecate frequently. A hummingbird will pass a meal of nectar from the crop into the intestine in only about four minutes, and transit through the intestines often takes less than 15 minutes. During this remarkably short time the bird can extract up to 99% of the ingested sugar glucose, due to the high number of glucose transporters in its intestinal tissue, quite possibly the highest density in any vertebrate and perhaps the maximum structurally possible for an intestinal membrane. This Magenta-throated Woodstar takes in the sugary secretions of a Poinsettia flower while simultaneously eliminating the waste products of nectar digestion. This species is common throughout its Central American range, feeding on an especially wide variety of plants in most habitats except dense forest and at all altitudes below 1500 m.

[*Calliphlox bryantae*,
Costa Rica.

Photo: Michael Fogden/
DRK]



on females of small species may explain why single annual broods are much more common in these species than in medium-sized to large ones.

The incubation period for the majority of trochilids lasts 16-19 days, about 2-5 days longer than in songbirds. The shortest periods known are for the White-eared Hummingbird (*Basilinna leucotis*) from Central America, at 14-16 days, whereas hillstars and other high-Andean species can attend the clutch for 22-23 days.

For the few species studied in detail females incubated during 75-90% of the daylight hours. How do these birds, which normally consume nectar every 6-10 minutes, meet their energy requirements during this prolonged stationary period? Some physiologists suggest that the metabolic rate of a bird at rest can supply all the heat required for incubation. Others conclude that the energy requirements for incubation must be supplied by supplementary heat production which would necessitate an increased food intake. A closer look at the thermoregulatory ability of incubating females reveals that they compensate for a reduced food intake during long attentive periods by reducing their body temperature from 41°C to about 32°C, resulting in energy savings of almost 50% during the day.

Depending on the timing of the start of incubation, eggs may hatch at intervals of 48 hours or almost synchronously. Hatchlings of all hummingbirds are altricial: nearly unfeathered, blind and helpless. During their long nestling period of 23-26 days, or in high-Andean trochilids 30-40 days, the following three well-differentiated morphological stages of development can be observed.

In the first, from day one to about day five after hatching, the nestling is nearly naked except for two dorsal rows of neossomite down about 5 mm long, and its eyes are still closed. During this stage the chicks, generally two in number, are inactive in the nest. When the female arrives with food she lands on the edge of the nest and touches the nestlings behind the eye-bulges with her bill. In response to this stimulus the young birds gape and

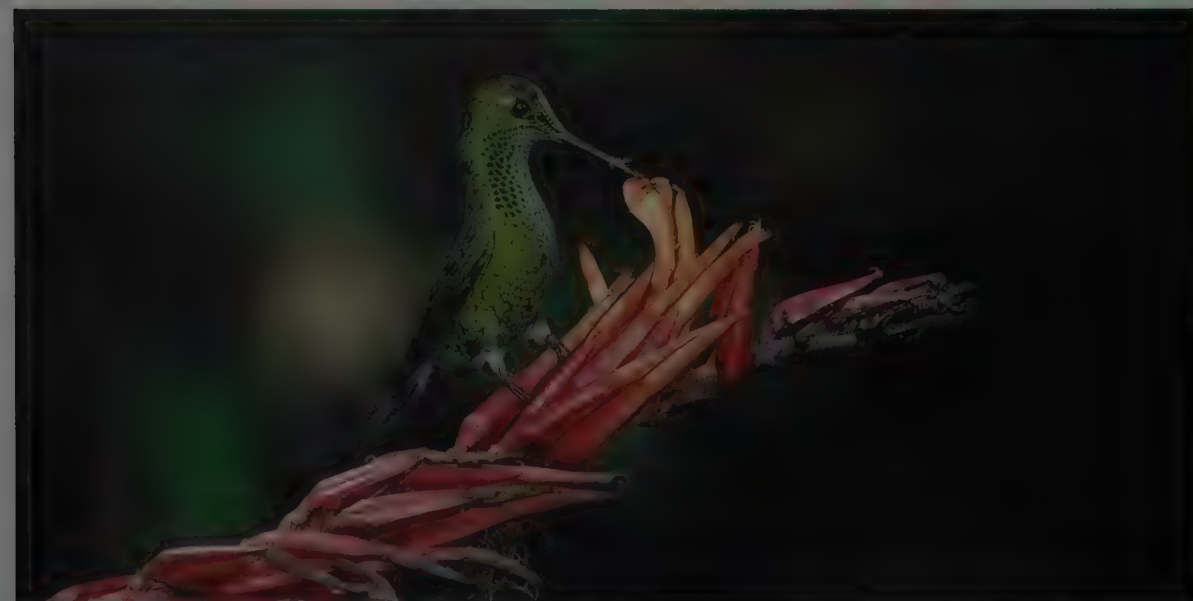
are fed by the female, which inserts her fine bill into each nestling's mouth and regurgitates food consisting of nectar and tiny arthropods from her crop into that of the chick. Gaping in nestlings of that age can easily be artificially induced several times by touching the eye-bulges with a matchstick. No begging call can be heard at this stage.

The second stage, from day six to day nine, when the eyes begin to open, is the period of major feather development on the wings, tail and back. The dorsal down is not shed but remains attached to the contour feathers. Begging calls are still not heard at this time.

The third stage of nestling development covers day ten until fledging, at around days 17-19. By the beginning of this period chicks are almost completely feathered and often sit on the edge of the nest facing outward, but they still fail to give begging calls.

During the second and third stages, the female gradually approaches the nest and begins to hover over the feathered young with an increased wingbeat frequency that is clearly audible. When the dorsal neossomite down attached to the chicks' contour feathers is visibly agitated by the resulting air movement, the chicks invariably begin to gape; gaping can easily be triggered in the chicks at this age of development by blowing with a straw on their dorsal neossomites. The gape-releasing stimulus during this stage of development has changed and no touching of the eye-bulges by the female can be observed. When gaping, and also during feeding, the chicks raise themselves only slightly and remain in a rather stooped position in the nest.

With increasing age, from about day 15 onwards, chicks often sit at the edge of the nest during the day, mostly with their backs turned away from the cup. At feeding time the female hovers just above the chicks, causing movements of their dorsal neossomite plumage, and only after this stimulus will the nestlings gape and then be fed. In all trochilids studied raised in an open cup-shaped nest, begging calls are still not heard at this



Feeding during hovering flight, this Buff-tailed Coronet pays an energetic cost while accruing nutritional benefits. To reduce energy requirements, hummingbirds usually take the opportunity to rest while feeding, sometimes maintaining balance with open wings as in this Fire-throated Hummingbird, but ideally with their wings closed and at rest, like this Green-fronted Brilliant. Hummingbirds spend over 70% of each day perching, partly to offset their flight costs, but also because it takes around four minutes to empty the nectar-filled crop into the intestine. As a result, hummingbirds that have filled their crops with food are forced to delay foraging until space is available. They are thus unable to exploit nectar resources any faster, and have even been observed feeding at four-minute intervals.

[Top: *Boissonneaua flavescens tinochlora*, Ecuador.
Photo: Michael Gore.

Middle: *Panterpe insignis*, Costa Rica.
Photo: Michael & Patricia Fogden.

Bottom: *Heliodoxa jacula henryi*, Monteverde National Park, Costa Rica.
Photo: Adrian Warren/Ardea]

nestling stage. When the dorsal down from laboratory-reared hummingbirds was removed with forceps on day 10 after hatching, gaping reactions were not elicited by the female's hovering closely over their backs. However, when a hovering female landed on a chick's back it gaped immediately and was fed. Two days after the neossoptile plumage had been removed, gaping reactions could once again be observed with the approach of the female. The absence of tactile stimulation suggests that optical signals may by then have become adequate stimuli. Begging calls are given by hummingbird chicks only after fledging. They normally give loud begging calls, irrespective of the presence of the female, but call more vigorously when she is in view.

Because hummingbirds forage by hovering they can no longer climb with their feet, which serve only for perching. Consequently, they build exposed but camouflaged nests easily accessible in flight. The often exposed nest-site and low reproductive output probably favoured the development of the highly specific gape-response behaviour. Loud begging calls of the offspring, as well as uncontrolled begging and gaping movements through non-specific causes like vibration of the nest by wind, would be types of behaviour that could potentially betray the nest-site to predators such as tree lizards, snakes and birds. Thus, the highly specific stimuli which elicit gaping by unfledged hummingbird chicks are most likely adaptations for reducing predation on exposed nest-sites. Consistent with this observation is the fact that chicks of those hummingbirds like sylphs and metaltails which build domed nests give begging calls very shortly after hatching, presumably in response to tactile stimuli from the female as she enters the nest.

As part of a predator-avoidance strategy female hummingbirds never approach the nest directly. They often fly to the nest-site in fast semi-circles or with zigzag manoeuvres. A surprising form of anti-predator behaviour has been observed independently by R. Cintra and K. L. Schuchmann in the two species of fairy (*Heliothryx*). When leaving the nest after each brooding or feeding period, the female, with wings and tail fanned out horizontally and with only very slight aerodynamic corrections, performs a spiral gliding flight into the understorey. This downward movement strikingly resembles that of the falling dead leaves seen continually in humid tropical forests. When both gliding patterns, that of the bird leaving the nest and that of the falling leaves, were compared with regard to their velocity, identical speeds were recorded. The gliding flight posture and speed of *Heliothryx* most likely mimics falling leaves and protects the nest, nestlings and adult against predation.

When leaving the nest, females of the White-necked Jacobin exhibit a moth-like flight with rising and falling manoeuvres. This behaviour may be interpreted as a distraction display because it is conspicuous, attracting attention to the bird itself rather than to the nest.

Female hummingbirds feed their young throughout the day roughly twice per hour, and brood them until an age of 7-12 days. Studies of thermogenesis in nestlings involving the Reddish Hermit and the Blue-throated and Broad-tailed Hummingbirds indicate that the development of thermal control falls into that period. Thereafter, the young can regulate their body temperature and metabolism and do not depend on extra maternal warming.

Hummingbird nestlings grow quickly, reaching almost 80% of their adult mass within 10-12 days. For a minuscule organism like a chick the use of nutrients for fast attainment of heat-retaining tissue may be of greater selective advantage than its employment for maintenance functions. However, unfavourable weather conditions may retard development and extend the required nest period for several days. Weather conditions actually have a strong impact on nestling mortality during the days when internal temperature control mechanisms are still undeveloped. In the few studies where nesting success has been monitored in tropical species, figures vary from 20% to 40%, while some high-Andean trochilids (*Oreotrochilus*, *Oxypogon*) are exceptional with success rates of around 60%. About 30% of nestling mortality in tropical species is attributable to predation, whereas adverse climatic conditions contribute to the majority of all losses. The reverse is the case in some North American trochilids (*Calypte*, *Archilochus*), where similarly low nesting success is known, except for the Broad-tailed Hum-



mingbird from the higher altitudes of the Rocky Mountains, with 60%. According to these studies predation accounts for most of the mortality during reproduction.

Female hummingbirds may occasionally be seen at nests with young that are not their own. Violet-ears (*Colibri*) have been reported to feed nestlings and fledglings of White-eared Hummingbirds and trainbearers (*Lesbia*). The Brazilian hummingbird specialist A. Ruschi observed, in his aviary, a female Planalto Hermit (*Phaethornis pretrei*) which adopted a nestling of the same species whose mother had died. However, normally females chase any visitor to their nest away.

At the age of 15-18 days, a few days before fledging, nestlings are much more active in the nest, and they will preen their plumage for extended periods and look around with interest when other birds or the parent are near the nest.

After leaving the nest the young are fed by the mother for 18-25 days, in some tropical genera like fairies and sylphs occasionally for up to a month. Juveniles do not follow their foraging parent but remain in a particular place for several days, often high up in the tree tops, where they are fed by the female. When they are flying well, often shortly after the fifth day after fledging, the female prolongs the feeding intervals, teaching the young by loud calls to come for food wherever she wants to feed them. By doing so the juveniles quickly learn to follow the parent bird to her feeding grounds in flowering shrubs, vines or trees. Foraging for nectar is the next step for the young to learn, and this is

Male hummingbirds are generally polygamous, associating with the females only briefly during the reproductive cycle and then only for the purpose of courtship and fertilization. This generally occurs in a short period of sexual synchronization wherein males advertise for mates by vocalizing and display their plumage to advantage. This sometimes entails gathering at communal or diffuse lekking grounds, as with the Phaethornithinae, but more frequently it involves prolonged and solitary calling from within territories to attract receptive females, which invest so much in parental care that they are choosy in their search for mates. The resultant competition between males for access to females selects for brilliant plumage and elaborate displays. The Frilled Coquette, for example, erects a rufous crest, fans a glittering emerald throat, and raises the mantle feathers to show off a white rump band, all to charm his prospective mate.

[*Lophornis magnificus*.
Photo: C. H. Greenewalt/
VIREO]



All parental duties, such as nest building, incubation and rearing of the young are carried out solely by females, like this Rufous Hummingbird collecting nest material from a bullrush. There are occasional reports of males assisting at the nest during the incubation or feeding stages, but most cases are probably due to misidentification. Nest building in hummingbirds generally takes between five and ten days, with most effort being invested during the morning, and very little after mid-afternoon. Females of this species, however, along with most other North American hummingbirds, tend to continue nest construction throughout the day. After initial completion, females regularly repair and add to nests through the breeding cycle.

[*Selasphorus rufus*,
British Columbia, Canada.
Photo: Günter Ziesler]

mainly achieved by observing the adult at close quarters when she is sampling nectar. However, this period of learning to choose the right food is often based on trial and error. Several days before juveniles achieve independence they show mutual agonistic behaviour, often attacking each other with their feet, trying to prevent the brood-mate from being fed. Between feeding bouts, young hummingbirds are often seen to probe at twigs or red parts of leaves which resemble flowers in shape and colour. This exploratory behaviour is maintained throughout adolescence and ultimately leads them to new nectar sources.

Female hummingbirds may successfully rear two broods in a season, and in some North American species nest building and even incubation have been observed while the female was still attending nestlings in her first nest. For several tiny tropical species (*Chaetocercus*, *Lophornis*) one brood only seems likely to be the limit, for energetic reasons. Generally all species will attempt to nest a second or third time if their initial clutches or broods are lost at an early stage of reproduction.

Although the effort of reproduction causes severe physiological stress to adult females, their typical lifespan of 6-12 years seems to be similar to that of males, which of course play no part in nest building or rearing the young. The average maximum age of free-living trochilids seems to be about five to eight years. In the wild, one Blue-throated Hummingbird was known to be 12 years old, and a ringed Ruby-throated Hummingbird was trapped in the Rocky Mountains when aged 11 years, while captive birds have been known to live some years longer (see Relationship with Man). Although few data are available on the annual survival rate, information from North American species indicates a rate of between 40% and 50%.

Movements

Few members of the Trochilidae make substantial seasonal movements that could be called true migration. The species embarking on such journeys are those whose breeding grounds lie furthest north or south of the tropical zone, among them the world's smallest long-distance avian migrant, the Calliope Hummingbird (*Stellula calliope*). Many more species undertake post-breeding dispersal, altitudinal movements connected with food supply or

climate, or nomadic wandering in search of nectar sources. The hermits are generally less mobile than the trochilines.

In fact, very little is known about hummingbird movements; few species have been the objects of systematic ringing projects and most speculation remains based on data that are little more than first and last records at a given locality or regular appearance and disappearance in some area or another. Where they come from or go to, or in what age- or sex-classes they move are matters that are entirely unknown for the majority of species. Although long-distance migration by hummingbirds is rare, F. G. Stiles has pointed out that migratory or nomadic behaviour is more pronounced in nectarivorous birds than in those of virtually any other trophic category.

Since all hummingbirds depend on nectar throughout the year they must ensure that a ready supply of the appropriate flowering plants is available. Within the tropics this supply is year-round and constant, each species only having to find "its" food plants, and as a result the great majority of all tropical lowland trochilids are more or less sedentary. For montane species breeding at high elevations, this search for nectar-rich flowers and their associated tiny invertebrates can require a regular seasonal movement to lower altitudes, often to coastal regions. Surprisingly, some high-Andean species remain at the highest elevations throughout the year, as for example the hillstars (*Oreotrochilus*). They all breed at up to 4000 m or 5000 m, often right to the snow-line. Nests are typically sheltered by rocks or on buildings, while food plants include cacti, spiny shrubs and cushions, or *Puya*, a spiky bromeliad; they also need to take many arthropods. Some hillstars do move to lower altitudes but only in the severest conditions.

Little is known about the movements of hummingbirds nesting in the high southerly latitudes of South America. The Green-backed Firecrown, with a breeding range extending to Isla Grande of Tierra del Fuego at around 54° S, migrates northwards for the austral winter mainly to the lowlands of Argentina, reaching as far north as 23° S. The nominate race of the Giant Hummingbird, breeding in southern and central Chile and western Argentina, traverses the Andes to milder lowland Argentina in the autumn.

By contrast, there is a comparative wealth of information on the migration strategies of North American trochilids. Most migratory hummingbirds are partial migrants: only some of the population undertake movement, often those at the northern lim-



Most trochiline nests are tiny cup-shapes attached to branches or forked twigs, although pendular and domed structures are built by some species. Female trochilines tend to select breeding sites in the vicinity of prime foraging areas.

They visit appropriate sites, often hovering over them and perching on them repeatedly.

This Rufous-tailed Hummingbird has started the process of nest building at its chosen site in a low shrub by creating a platform of strong twigs, then adding softer material to form a cup. It nests practically all year round in much of its range from central Mexico to western Ecuador, except during the annual moult.

Seasonality of nesting is mediated by environment, those birds breeding at high altitudes or latitudes tending to be strongly seasonal while species from tropical lowlands often appear non-seasonal when local conditions allow. It has been found that nest architecture is a useful phylogenetic tool in the group as for the eleven trochiline groups proposed, nests show typical patterns for each assemblage.

Unfortunately, nest descriptions for several key taxa are not yet available, so further research is required.

[*Amazilia tzacatl*.
Photo: François Gohier/
Ardea]



When completed, the Purple-throated Carib's nest is small relative to the size of the bird, a soft compact cup of plant fibres woven with strips of bark, moss or lichen to camouflage the exterior. This species, like a few others, has an interesting resource-based mating system, in which females are allowed into male feeding territories that are otherwise rigorously defended, and they tend to mate with males that have appropriated the highest-quality resources, visiting these when feeding their young. The female herself is highly territorial around the nest-site, attacking much larger species that venture too close.

[*Eulampis jugularis*,
Le Lamentin, Martinique.
Photo: Robert Tyrrell]

its of the breeding range, while others are sedentary. Among the species that vacate their entire breeding range in North America are the Ruby-throated, Black-chinned (*Archilochus alexandri*), Calliope and Rufous Hummingbirds.

On their autumn and spring journeys between southern Canada and the eastern USA and Central America many Ruby-throated Hummingbirds make an astonishing crossing of the Gulf of Mexico, a one-way trip of 800-1000 km. They appear to migrate in troops of varying sizes, travelling low above the water; A. C. Bent describes how in a high wind Ruby-throated Hummingbirds were observed flying between the waves of Lake Erie, and on another occasion about 8 m above the waters of the Gulf of Mexico. Males arrive first both in spring and autumn, followed by females then juveniles, with about a week between them all, a pattern also noted for other hummingbird species. Most birds however follow the coast of the USA and Mexico rather than crossing the Gulf. Arrival on the breeding grounds in the north in about early May is possibly timed to follow on the appearance of the migratory Yellow-bellied Sapsucker (*Sphyrapicus varius*), since the hummingbird can feed on the tree sap exposed by this woodpecker (see Food and Feeding), while arrival in Arkansas is said to be synchronized with the flowering of the dwarf buckeye shrub (*Aesculus parviflora*), a favourite nectar source. The timing of the autumn overland movement during August and September coincides with the peak occurrence of jewelweed (*Impatiens biflora*) flowers.

Some of these northern breeders show a loop migration pattern, following different autumn and spring routes when migrating. For the Calliope Hummingbird, between its breeding grounds in the western USA and south-west Canada and its winter quarters in south-west Mexico, these round-trip distances can be up to 4500 km and 5500 km respectively. On the basis of both ringing records and museum skins, movement in autumn appears to be principally along the Rocky Mountains, with the northbound spring movement further west and at a lower altitude, along the Pacific coast. A few ringing recoveries point to individuals following the same route each year. In contrast to the Ruby-throated, the Calliope Hummingbird seems to migrate singly and not in groups.

The Rufous Hummingbird breeds further north than any other member of the Trochilidae, at 61° N in Alaska. If the distance between this extreme point and the south of its wintering grounds in central Mexico is measured in body lengths, then this species holds the world record for the longest migration performed by any bird. It follows an elliptical route very similar to that of the Calliope Hummingbird: in July and August southwards along the Coast Ranges and Sierra Nevada in the west, and the Rocky Mountains further east (where it is common at nectar sources at up to 3000 m, exceptionally 4000 m), avoiding the Great Basin Desert between, with return migration from January following the Pacific coast to arrive in north-west North America around April. The species is present on its breeding grounds for one of the shortest periods recorded in the Trochilidae. The mean body

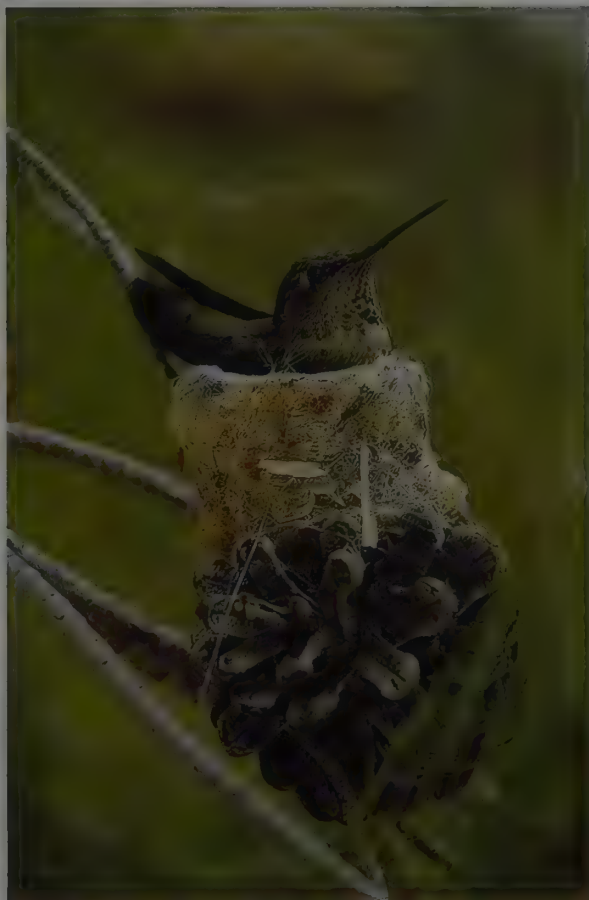
Various materials are used by hummingbirds in nest construction. After clinging to a suitable looking leaf-tip, a female hermit selects a nest-site upon which she attaches material to construct a cone-shaped nest. Depending on the strength and angle of the leaf, hermits, like this Straight-billed Hermit, often attach ballast, such as pieces of clay and pebbles, to maintain stability and ensure that the cup is horizontal. The nests of trochilines are often made of moss and plant fibres, as in the case of this Violet-headed Hummingbird, while an inner layer of small feathers, animal hair and other soft material forms an insulating lining. The entire structure is often bound together by spiders' webs, many species decorating the outer surface of their nests with material that functions as camouflage; this Ruby-throated Hummingbird (bottom left) has used lichen and bark for this purpose. Nests tend to be saddled on branches and forked twigs or placed on large leaves, although many different sites have been recorded. The nest of this Anna's Hummingbird, for example, is perched on top of a pine cone. The tendency of this species to nest during winter, the incubating female often being exposed to heavy frosts or snow, has probably developed to reduce competition with other hummingbirds that visit the coastal Californian scrub zone during spring to breed.

[Above left: *Phaethornis bourcierii bourcierii*, Peru.
Photo: Michael & Patricia Fogden.

Above right: *Klais guimeti merrittii*, Costa Rica.
Photo: Michael & Patricia Fogden.

Below left: *Archilochus colubris*, Illinois, USA.
Photo: Richard Day/Oxford Scientific Films.

Below right: *Calypte anna*, Sonoran Desert, Arizona, USA.
Photo: John Cancalosi]





The White-necked Jacobin positions its nest on top of *Geonoma* palm fronds. When leaving the nest, females of this species perform a strange moth-like flight, with curious rising and falling movements. This is thought to relate to nest protection, possibly by drawing the attention of potential predators away from the nest-site itself. When predators are detected close to nests, hummingbirds mob them directly using dive-bombing flights accompanied by frantic distress calling.

[*Florisuga mellivora* *mellivora*, La Selva Biological Reserve, Costa Rica. Photo: G. I. Bernard/NHPA]

mass of trapped birds on spring migration was 3.27 g, in autumn 3.44 g, the most likely explanation for the difference being that birds cover the northward journey in shorter stages to avoid being earlier than the opening of their nectar flowers at any place *en route*. Birds have been recorded arriving in the state of Washington at the end of February, a time when the last stragglers are just leaving Mexico, and the advance birds must try to survive on aphids and midges. In Oregon, the arrival of the bulk of the birds is said to coincide with the blooming of the currant *Ribes sanguineum*.

Allen's Hummingbird also follows an elliptical flyway, southward through Arizona and central Mexico but in spring further to the west; the first birds begin to move south already in May, the earliest departure of any North American trochilid, while the last have left California by early October. Again, adult males migrate about two weeks before females and a month before juveniles. Arrival in Mexico is from August, some departing in January to establish territories by mid-February. Another likely loop migrant is the Broad-tailed Hummingbird, which breeds in the southern and central Rocky Mountains, most probably following the same elliptical south-east, west, north route to and from Mexico.

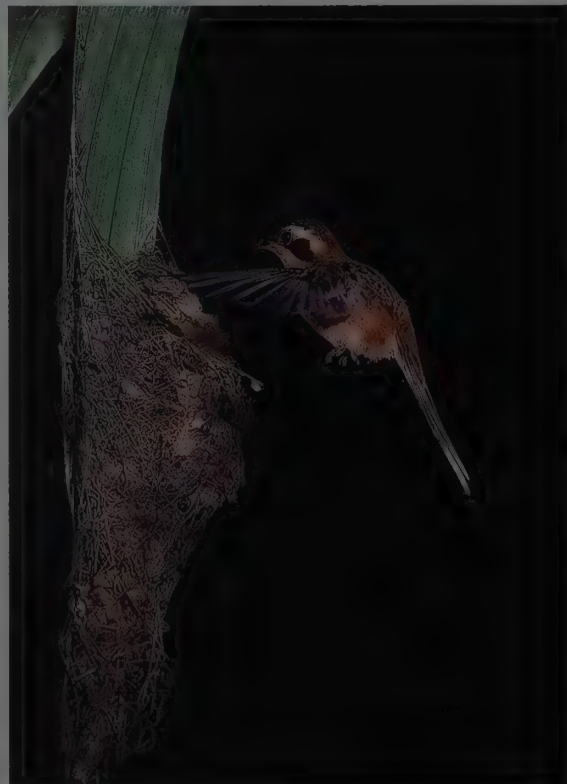
The energetic problems raised by the long-distance movements of these tiny birds, in particular the non-stop flight of the Ruby-throated Hummingbird across the Gulf of Mexico, remained something of a puzzle for many years. It used to be thought that this species had a metabolic rate in flight of 80 cm³ of oxygen per gram per hour, which meant that if they carried an extra 2 g of fat they would still only be able to cover a maximum of about 620 km and hence could not cross the Gulf. However, later experiments showed that the average metabolic rate was actually considerably lower at 42 cm³ of oxygen so that, flying at 40 km per hour, they would have energy reserves sufficient for about 25 hours of flight or a distance of 1000 km.

Like other migratory birds, trochilids have to accumulate body fat as an energy store in order to cover long distances without feeding. The Ruby-throated Hummingbirds taking the route across the Gulf of Mexico must double their body mass to around 6 g, while increases of up to 59% have been recorded for Broad-tailed Hummingbirds immediately before they set off southwards, and in Anna's Hummingbird a maximum body-mass increase of 48% in males and 44% in females has been measured in October.

Ring studies carried out in Brazil have shown that there are seasonal north-south movements within the tropics. Individuals of the Ruby Topaz (*Chrysolampis mosquitus*) marked in the state of Paraná were retrapped around 1000 km to the north-east; the species appears to leave the Rolândia region of Paraná in

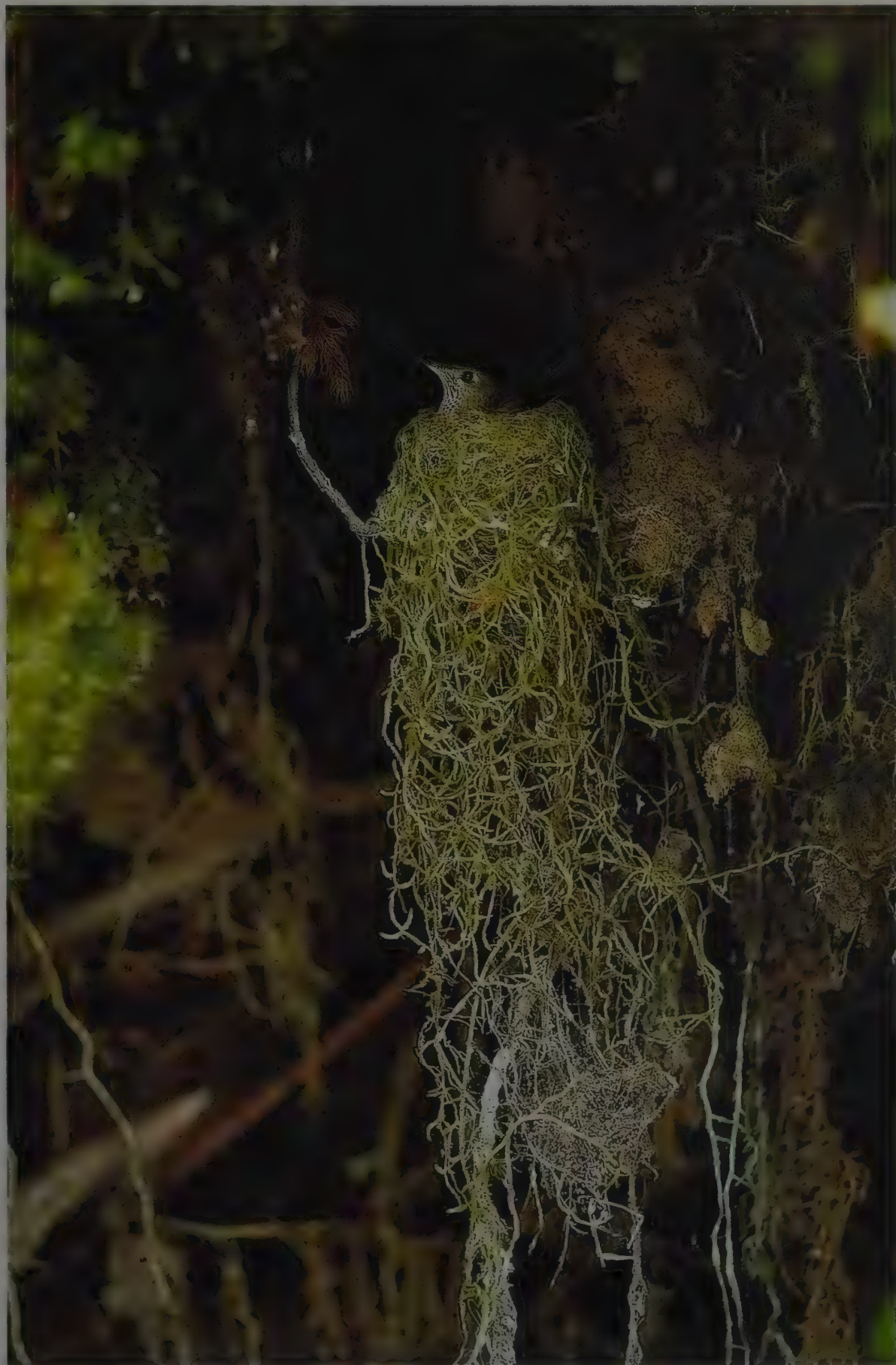
April, during the austral autumn, returning annually on almost the same date in mid-October.

The two *Calypte* species, Anna's and Costa's Hummingbirds, illustrate well how difficult it can be to unravel hummingbird movements. Anna's breeds along the coastal region of California, leaving in about June-July. The birds either move the relatively short distance into the mountains behind, some to altitudes of over 3000 m, though when mountain temperatures drop in the autumn many return to lower elevations; or they cover the much greater distance to the south and east as far as northern Mexico and New Mexico. The two movements seem to be different: the first is a form of post-breeding altitudinal dispersal; the second is true migration. Winter site-fidelity has been noted in Arizona



Nests of the Phaethornithinae differ markedly from their trochiline relatives, lending weight to the morphological evidence for their separation at the subfamily level. The Reddish Hermit, like all members of the assemblage, constructs a pendant, compact, cone-shaped nest, most often attaching it to the inner tip of a hanging palm or Heliconia frond, but sometimes fastening it to a vertical root or twig, if suitably sheltered. Unlike trochilines, hermits tend not to nest in the proximity of rich feeding patches. This species, one of the smallest birds in the world, has been reported using a wide variety of materials in nest construction.

[*Phaethornis ruber ruber*, Montsinéry, French Guiana. Photo: Jany Sauvenet/NHPA]



Very few nests of the Green-backed Firecrown have been described, but the species is known to prefer sites that overhang water and to build the small cup typical of most trochilines. This design is at least occasionally draped in impressive amounts of extraneous material for the purposes of camouflage. Balanced microclimatic conditions, such as temperature and humidity, are apparently essential to the successful development of hummingbird embryos, and, for this reason, nests are usually placed out of direct sunlight or adjacent to waterfalls. The breeding season of this species falls between September and December in the austral spring, as its breeding range is otherwise beset by very low temperatures.

[*Sephanoides sephaniodes*, southern Chile.
Photo: Günter Ziesler]



with ringed individuals being trapped in subsequent years. Anna's Hummingbird has been described as having no winter range as such and its migration is rather a series of temporary residences wherever flowers or feeders are available.

Costa's Hummingbird is a bird of desert and other dry places, with three principal breeding habitats in the USA and three different migration strategies. Almost all of those breeding about March-April in the Sonoran Desert scrub of Arizona and California depart in summer, males a month or so earlier than females and immatures. They appear to move to the coast of California and north-west Mexico, though this is not easy to ascertain because of the resident population already present in the region. The migrants return to their breeding grounds in October and November when the desert lavender *Hyptis emoryi* (Labiatae) starts to flower. In contrast, the birds inhabiting the desert scrub of California, Nevada, Utah and Arizona undertake post-breeding movements around June, some to higher elevations in the coniferous forests of the eastern Mojave Desert but most apparently southward to Mexico. In the coastal scrub and chaparral of southern California breeding birds are present between March and September. There is an increase in numbers in late April, possibly from the Sonoran Desert population, some of which conceivably arrive to breed for a second time. Many spend the winter in gardens but most presumably leave for Mexico. Post-breeding vagrancy has been recorded north to southern Canada and to eastern Texas.

Other ringing studies have shown varying degrees of site-fidelity within the Trochilidae to both breeding and wintering grounds. Of 188 male Magnificent Hummingbirds ringed on their breeding grounds in Arizona, 41% returned in subsequent years, as did 23% of 60 females ringed. Of 1224 Ruby-throated Hummingbirds, 130 (39 males, 91 females) were retrapped, while none of those ringed in winter in Louisiana was subsequently recovered, though in Costa Rica 2 of 14 ringed there were later recaptured. That the birds can also closely follow the same flyways is shown by the 96 male and 161 female Anna's Hummingbirds trapped on autumn migration in south-east Arizona: 35.4% and 23.8% of them respectively had been captured there in the preceding two years. In the Broad-tailed Hummingbird, up to 56% of females and 29% of males ringed as adults in summer subsequently returned, though only up to 22% of 146 birds ringed as

juveniles turned up again at their natal sites. Twenty Rufous Hummingbirds were retrapped up to four years after ringing at the same winter sites in Mexico.

Ringing work has also thrown light on the sorts of distances individual hummingbirds will cover within their home ranges. In their breeding quarters, males of course move around searching not only for food but also for females. In Costa Rica, marked individuals of a number of species moved distances of approximately 0.5-1.5 km to defend feeding territories at flowering trees and plants in peak bloom between February and August. One male Violet-headed Hummingbird was recorded in two consecutive years moving from a *Stachytarpheta* (Verbenaceae) shrub to a *Warszewiczia* (Rubiaceae) tree when it was in full flower then back again, and a male Fork-tailed Woodnymph (*Thalurania furcata*) moved about 1.5 km in three days to a richer stand of the same *Heliconia imbricata*. In the Rocky Mountains in summer, Broad-tailed Hummingbirds were recaptured at up to 6.7 km away from their release points. Between March and July in Arizona more than 100 male Magnificent Hummingbirds were marked but only a few were noted again, showing a high degree of mobility. In contrast, 12 Rufous Hummingbirds were recaptured at the same wintering site in Jalisco, Mexico, after an average of 32 days, indicating only short-distance foraging movements. In Brazil, a ringed Black Jacobin traversed an elevational difference of 455 m and a distance of 30 km inside a day while searching for nectar sources.

Also in Brazil, displacement experiments by A. Ruschi have shown that many hummingbird species have a strong navigational ability, which is perhaps not altogether surprising, since, being entirely dependent on particular flowers, they must know where to find them within their feeding areas. Ringed individuals of the Planalto Hermit, Black Jacobin and Black-throated Mango (*Anthracothorax nigricollis*) were transported 85 km to the coast then released; all of them returned to where they had been trapped, at an altitude of 700 m, the hermit covering the distance in just two and a half hours! By contrast, other ringed individuals of the Minute Hermit (*Phaethornis idaliae*), Frilled Coquette and Brazilian Ruby (*Clytolaema rubricauda*) were unable to find their way back from a distance greater than 15 km.

Much of our picture of trochilid movements has been constructed from casual observations of species appearing in an area for a period of time at regular intervals, generally coinciding with the flowering of particular plants. The Horned Sungem (*Heliactin bilophia*) is among the most nomadic of the central Brazilian hummingbirds. It is a bird of open *cerrado* and scrubland and has recently colonized parts of the country where the forest has been cleared. It becomes very much commoner in the Distrito Federal between March and May because this is the peak flowering time there for Verbenaceae and Labiatae, *Hyptis* in particular. Nevertheless, some individuals are observed there outside this period, indicating the existence of resident and migrant populations. The Black Jacobin is present in Rolândia from March to September (hence its local name of "winter hummingbird"), but a little further north, in Rio de Janeiro State, the species is absent in the winter, generally appearing only in October. In São Paulo, there is a considerable hummingbird influx in March and April, when *Eucalyptus* blooms, most birds departing again during the austral winter. In Costa Rica, the White-necked Jacobin disappears from inland sites on the Caribbean slope between August and the end of November, but simultaneously becomes commoner at the coast. Marking programmes are necessary to confirm that individuals are actually moving from one place to another.

Near the Pacific coast of central Mexico researchers found that a feeding guild of 21 hummingbirds was composed of three broad groups, each with a different foraging strategy involving movement of differing types: one consisted of resident birds, each species or genus using its own particular habitat all year round; a second was made up of nomadic species, each utilizing several habitats, wandering from one to another, tracking the flowering of food plants; and the third was of migratory species, present in the area solely in winter. The resident species were territorial, defending their nectar sources, and the nomadic species were trappiners, while the migrants were also territorial, though since the food plants "left over" for them by the other two groups provided a rather scant diet they also took many insects.

Nests of montane trochilines are often bulky structures of moss and lichen, held together with spiders' webs and placed in sheltered positions under tussocks or against rocks. Those that nest at altitudes up to 5000 m, such as the Andean Hillstar, attempt to control microclimatic conditions by building highly insulated nests in windless positions. The large, woolly nests of this species are often glued to sheltered rock surfaces, especially in caves where several females may nest semi-colonially. The hillstars are the only group of hummingbirds in which territorial roles are reversed, the female performing the territory defence.

[*Oreotrochilus estella bolivianus*, Lauca National Park, Chile.
Photo: A. de Sostoa & X. Ferrer]



The Giant Hummingbird often simplifies nest protection by breeding in cacti, where sharp spines deter all but the most stubborn of terrestrial predators. The structure is composed of moss and lichens, lined with animal and plant wool, and is generally built in very open situations, often at the top of a cactus.

This aggressively territorial species is, as its name suggests, the largest member of the family. It is swift-like in size and flight action, travelling rapidly through the air using unusually slow beats interspersed with short glides. It is not uncommon throughout its pan-Andean range, usually frequenting open habitats with low vegetation. It gathers in particular at flowering Agave plants and Opuntia cacti for foraging, at which time it usually clings to the food plant in preference to hovering, presumably because its size imposes energetic constraints. It also visits exotic flowers in gardens and occurs regularly in the parks of major Andean cities, such as Quito.

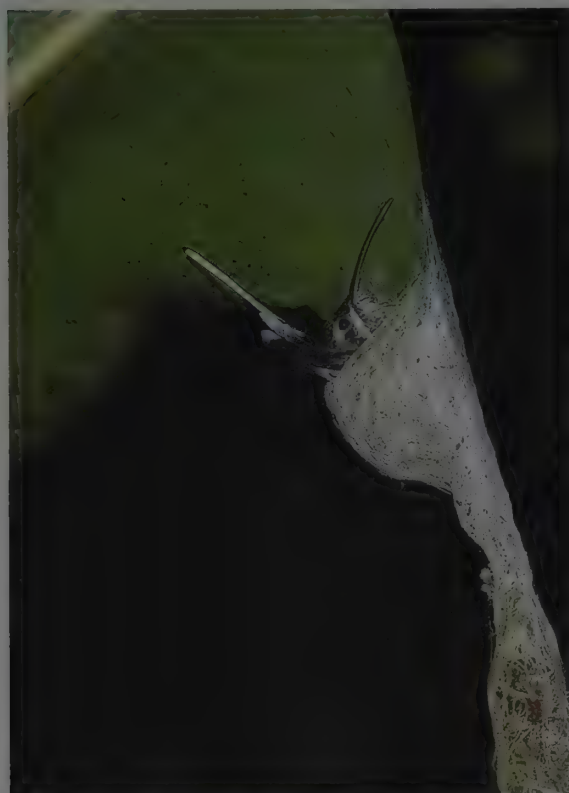
[Above: *Patagona gigas peruviana*, Argentina.

Photo: Günter Ziesler/
Bruce Coleman.

Below: *Patagona gigas peruviana*, Apurímac, Peru.

Photo: Günter Ziesler]





The complexity of hummingbirds' movements at a single location harbouring many species was vividly shown in a two-year study carried out at a site 1000 m up in pre-montane rainforest on the Caribbean slope of Costa Rica. Out of a total of 22 hummingbird species, a core group of 14 was examined in detail, ten of which were resident and four non-resident. The peak in total numbers was roughly from November to the end of July, followed immediately by the yearly population low point between August

and October, caused by a gap between the departure of visitors and the return of birds known or suspected to breed in the study area. November to March was the peak breeding period. There was a partial or complete downslope emigration from the area by residents mainly between June and September. For example, Coppery-headed Emeralds (*Elvira cupreiceps*) and White-bellied Mountain-gems (*Lampornis hemileucus*) descended to around 500 m, while Brown Violet-ears and Green Thorntails went down almost to sea-level, as did some immature Green Hermits, though during the period December-April. Non-altitudinal displacement was also observed, for instance the Green-fronted Brilliant (*Heliodoxa jacula*) was absent during June-July, probably visiting food plants outside the study area, namely *Heliconia latispatha* growing by nearby rivers. The non-resident birds appeared mainly in June-July early in the rainy season. They had apparently just bred elsewhere or were immatures; their immigration into the area seemed to coincide with the flowering of the shrub *Cephaelis elata* (Rubiaceae). Three of them, the Violet Sabrewing (*Campylopterus hemileucurus*), Green Violet-ear and Variable Mountain-gem (*Lampornis castaneiventris*) arrived from a higher altitude, while the Purple-crowned Woodnymph (*Thalurania colombica*) came from lower down the slope. Perhaps contrary to expectation, the peak flowering season at this site did not coincide with maximum breeding activity and the relationship between the two appears complex. The strongest correlation was for the Green-fronted Lancebill: the staggered flowering of five epiphytic shrubs, mainly Ericaceae, used as nectar-sources, generally coincided with important phases of the lancebill's annual cycle. A similar relationship seemed to exist between the Green Hermit and *Heliconia*, and the White-tipped Sicklebill and *Centropogon granulatus* (Campanulaceae), since the bird's appearance in the study area was associated with its blooming.

At a site on the same slope but at around 100 m above sea-level, the two peaks in flowering intensity, one in the dry season and the other in the first half of the wet, coincided with hummingbird breeding and moult respectively. The second of these is an especially critical time since the young have just fledged and a good supply of nectar is crucial. This abundance of flowering is succeeded by a low point in nectar availability from November to the end of January, when many trochilids leave the area, visitors from upslope as well as breeders. Observations in

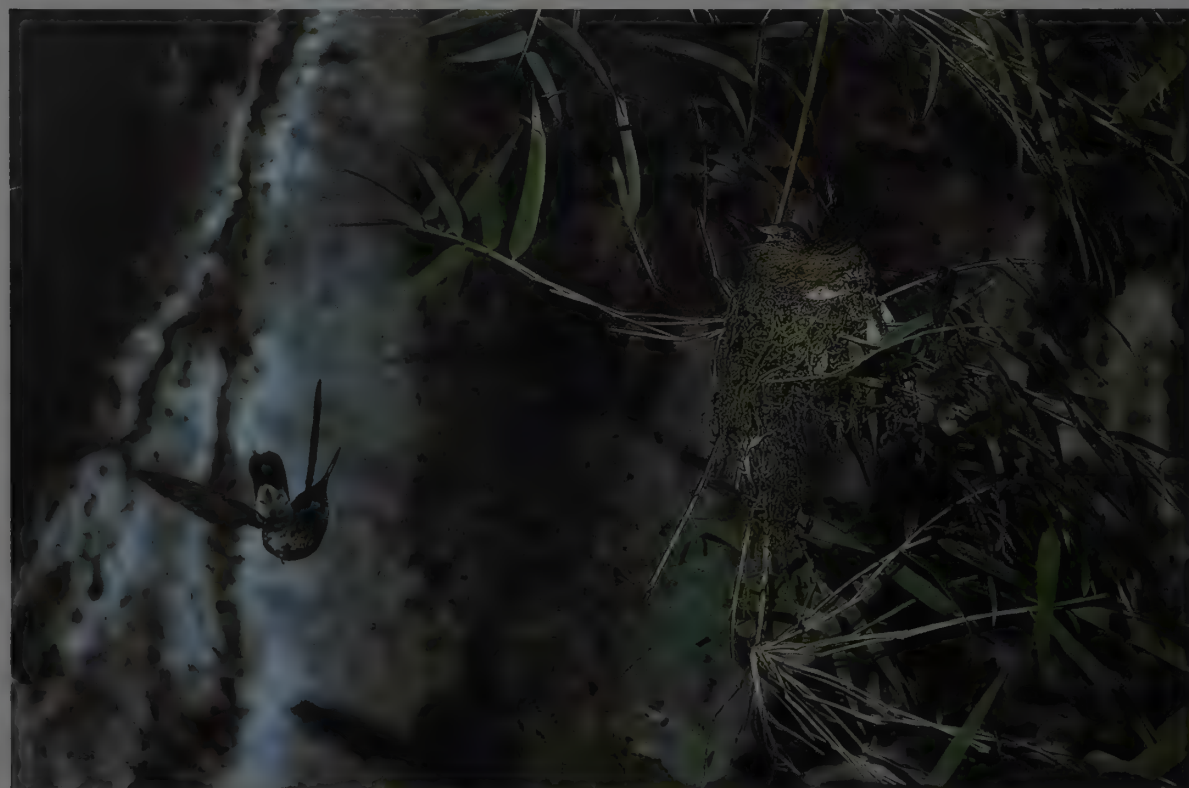
This Western Long-tailed Hermit has attached its nest to a banana leaf, constructing it mainly from plant fibres and cobwebs, and placing it in the leaf tip position typical of the Phaethornithinae.

In common with most other members of this subfamily, the female faces the leaf while incubating so that her tail points out of the open side of the nest.

One advantage of this nest design is that the overhanging leaf provides excellent protection from rain. Furthermore, the nest material allows free passage of water and quickly dries. These aspects are important, as showers are frequent and often torrential in the hermit's rainforest habitat.

[*Phaethornis longirostris baroni*,
Peru.

Photo: Günter Ziesler]



Females tend to start incubating irregularly after the first egg is laid, but they sit almost constantly once the second has arrived. Incubation itself lasts anything between 14 and 23 days, although most hummingbird eggs take 16-19 days to hatch. Incubating females compensate for a reduced food intake during incubation by lowering their body temperature, which results in an energy saving of around 50% per day. Although males have very little to do with the nesting process, this incubating Green-backed Firecrown was being investigated by a male.

[*Sephanoides sephaniodes*,
southern Chile.
Photo: Günter Ziesler]

The Black-chinned Hummingbird, like all members of the family, lays two eggs that are glossy white and oval in shape. Depending on the timing of laying, eggs might hatch almost simultaneously, or, as in this case, asynchronously, with a gap of up to 48 hours before the second egg hatches. The first stage of nestling growth lasts about five days.

During this time the nestlings are practically naked apart from two dorsal rows of neossophtile down about 5 mm long. Their eyes are still closed and they remain almost inactive in the nest. When the female arrives at the nest she touches one of the nestlings behind its eye-bulges with her bill, in response to which the nestling gapes and is fed.

[*Archilochus alexandri*,
Kickapoo, Texas, USA.
Photo: Sid & Shirley
Rucker]



these months of hummingbirds feeding at nectar-poor flowers highlight the difficulties faced by some species.

If a range of habitats within a particular area cannot ensure a reliable nectar supply at different times of the year then hummingbirds are forced either to move to where there is nectar or to adapt their annual cycle to the rise and fall of its abundance. Their varied and complex movements are in the main the result of hummingbirds maximizing their chances of access to nectar at different energy-demanding stages of their annual cycle, such as breeding and moult, but given the vagaries of climate short-distance movements by hummingbirds will often prove to be unpredictable.

Relationship with Man

Man's attitude to hummingbirds is a very unusual one within the context of his relations with the whole of the Animal Kingdom: it is wholly characterized by positive emotions, such as aesthetic admiration, affection and general amazement. As far as is known, hummingbirds have nowhere given cause for the degree of wanton persecution suffered by some other bird families: they are not crop pests; they do not compete with or harm domestic animals; they are not noisy; and there is not much eating on them, although, surprisingly, there is a south Brazilian dish called *passarinhos com polenta* with hummingbird as the chief ingredient! Apart from adding to the sum of human pleasure, they also carry out the important service of pollinating many of man's food plants, some of which have co-evolved with the birds; at least 58 plant families are pollinated by trochilids in Brazil alone, chief among them being the Bromeliaceae.

The persecution to which they have been subjected is rooted in their virtues. Since the earliest times they have been killed for their wonderful plumage, and more recently captured in huge numbers so that people can appreciate them even more at close quarters. Mankind has doubtless always been astonished by their unearthly iridescent colours, their acrobatic flying skills, and their sheer tininess. They are among the most mysterious creatures on our planet.

Our feelings towards these birds are well expressed in the names we have given them. Their English names parallel both those in other languages and the normally unpoetic scientific

nomenclature in attempting to capture some of the hummingbird magic: sapphire, emerald, goldenthrout, mountain-gem, jewelfront, brilliant, hillstar, sunbeam, starfrontlet, sunangel, woodstar, sungem, sylph, woodnymph and fairy. The Spanish name is *picaflor* (peck the flower), the Portuguese *beija flor* (kiss the flower). That trochilids are easily attracted to the vicinity of houses by garden flowers or feeding bottles containing sugar-water, and quickly become accustomed to people, only increases their attractiveness.

Native peoples throughout South America use hummingbird plumage in their adornment, and we can assume that they always have done. The esteem in which these minute glittering feathers were, and are, held is exemplified by the fact that the great ceremonial head-dress of the Aztec king Montezuma (Moctezuma) II, the main element of which is the long green uppertail-coverts of the Resplendent Quetzal (*Pharomachrus mocinno*), the sacred bird of the Maya and Aztecs, also contains many hundreds of trochilid feathers, interspersed with tiny platelets of gold. The Aztecs kept hummingbirds and other animals in special extensive zoos in order to have a supply of feathers and pelts for ceremonial purposes. In 1519 King Montezuma presented this royal symbol to his eventual conqueror, Hernán Cortés, who in turn gave it to Emperor Charles V as part of a fabulous Aztec treasure of gold, silver, jade, pearl and turquoise. After seeing this hoard in Brussels, the artist Albrecht Dürer wrote "I have never seen anything in my entire life that filled my heart with greater delight". The treasure can be seen today in the Museum für Völkerkunde in Vienna.

Huitzilopochtli, "hummingbird of the south", from "*huitzilin*" (hummingbird) and "*pochtli*" (southern), was actually one of the most powerful of the Aztec gods, associated with battle and human sacrifice, the bird being depicted actually feeding on the blood of sacrificial victims. Fallen warriors were metamorphosed into hummingbirds to accompany the sun on its daily journey for four years before returning to earth to feed on nectar for eternity. Huitzilopochtli had another special place in Aztec mythology as the bird which guided the people on their long trek southwards in search of a new homeland to the spot in present-day Mexico City where they built their capital Tenochtitlán.

The greatest of the gods, the feathered serpent Quetzalcoatl, wore a cape of trochilid feathers and a head adornment of flowers with hovering, feeding hummingbirds. The first ruler of the



Unlike hummingbird chicks raised in dome-shaped nests, such as sylphs and metaltails, those raised in open-topped nests do not beg vocally for food. These Western Long-billed Hermit chicks in Amazonian rainforest gape to receive food, but they do not produce the familiar begging calls of most birds. After the first stage of nestling development, the female uses a non-tactile method to induce gaping: she fans the dorsal down of chicks while she hovers. Until they are thus stimulated they remain motionless, even if their parent perches on the side of the nest.

[*Phaethornis longirostris baroni*,
Manu National Park, Peru.
Photo: Günter Ziesler]

unified Aztec kingdom was called Huitzilihuite, or "hummingbird feather", and during his reign in 1391-1415 he elevated Huitzilopochtli to the position of Sun God, the supreme power in the pantheon, a further member of which was the goddess of earthly pleasures, beauty and birth, Xochiquetzal, or "flower bird", and she too was symbolized by a hummingbird. Trochilid feathers were an important part of a bride's wedding dress in Mexico into modern times. The bird was also an integral part of the Aztec calendar. This is more important than it might appear because this highly complex system lay at the very heart of Aztec culture and cosmology. Representations of hummingbirds in stone can be seen throughout the Aztec archaeological sites. The hummingbird is present too in the mythology and artefacts of the South American peoples, particularly the Inca and Nazca of the Andes, but to a much lesser degree than in Mesoamerica. Some of the gigantic figures inscribed by the Nazca on the surface of the dry plateaux of Peru probably represent hummingbirds.

A multitude of stories has arisen from the fact that trochilids often appear with the rains, since the flowers bloom then, but of course they are credited in many legends, particularly in the dry south-west of the USA, with being rain bringers, so water vessels are commonly decorated with their image. The Hopi and Zuni peoples incorporate the hummingbird in their rain dances, and their inlaid jewellery of turquoise and silver features the birds as favourite motifs. In a Navajo legend, the first hummingbird was large, white and very greedy, so much so that it killed many flowers in its search for ever more food. The Creator was displeased and made the bird smaller and smaller to reduce its appetite, but in the process it also lost its song, whereupon the other birds in their pity asked the Creator to compensate the hummingbird with the most beautiful plumage of all, which he duly did.

Another Maya version of how the hummingbird Tzunum (clearly an onomatopoeic name) came by his colours tells how, although the bird originally had inconspicuous plumage, his whole pride was in his fantastic flying skills. However, on his wedding day he realized that his dull feathers were an inappropriate outfit and he was thrown into depression. The other birds saved the day by giving him fragments of their own plumage as wedding presents, which so moved him that he almost lost his voice. The Great Spirit was touched by the hummingbird's gratitude and allowed him to wear his nuptial splendour for all time.

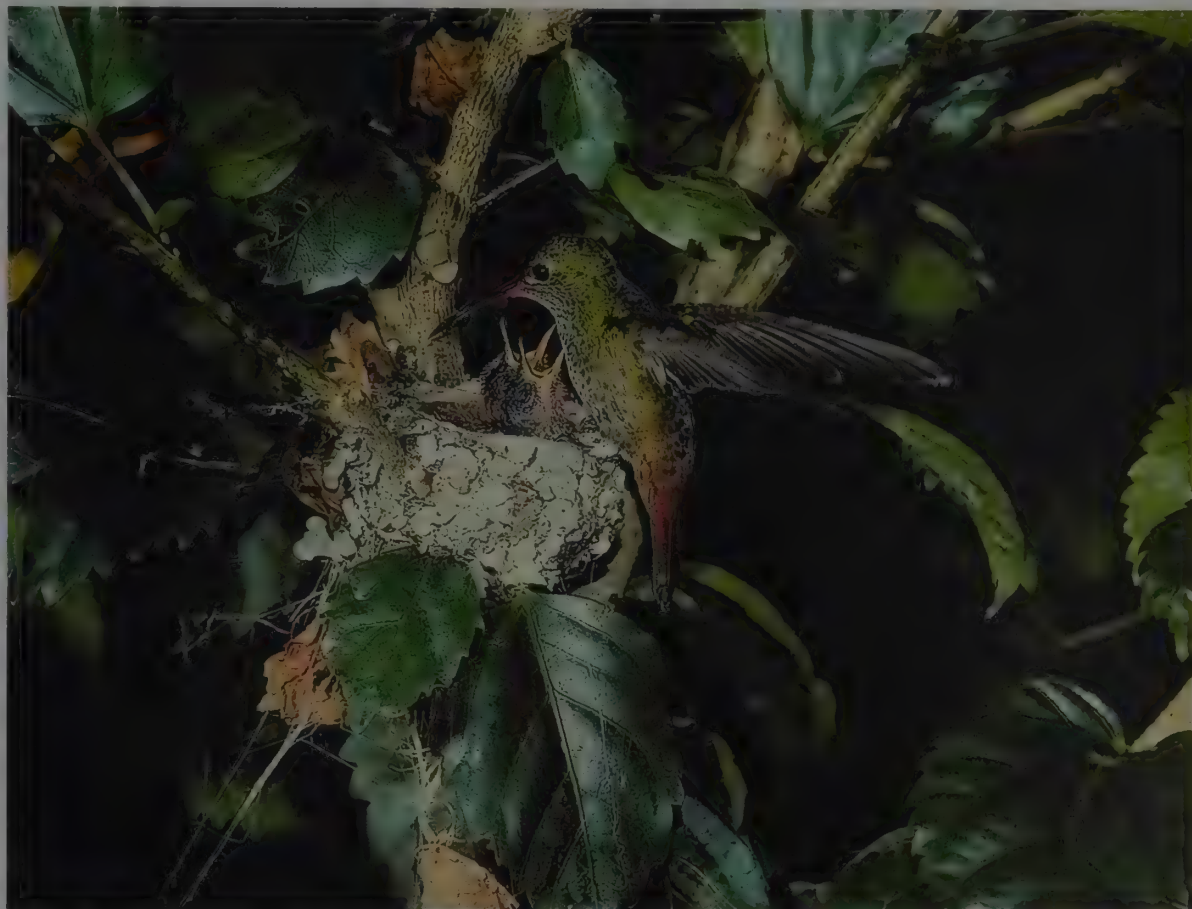
A different Maya legend relates how there were tiny scraps of material left over after the Great Spirit had created all the birds. Not wishing to throw them away he used them to make a hummingbird pair, which thus came to be composed of all the colours. The sun too wished to make a contribution so he gave his light, and since then hummingbird feathers have shone and glittered.

A belief in the special position of trochilids survives today in the form of superstition and folk medicine. On the whole hummingbirds, and also their nests, are regarded as bringers of good luck. In Costa Rica, dried and perfumed nests are hung around the neck, on belts, or nowadays in cars, as lucky talismans. In Mexico, amulets containing mummified or powdered hummingbirds can be bought in markets to bring good luck or success in love. The life-long fidelity of an unwitting partner can be secured by boiling up a dried hummingbird, including feathers, in a soup or stew, or by sprinkling the ashes of a hummingbird heart



The female Blue-tailed Emerald, like most hummingbirds, inserts her bill into the nestling's gape, regurgitating a fine mixture of nectar and arthropods. Hummingbird chicks take 23-26 days to fledge, although this is increased in high-Andean species to 30-40 days, as the low temperatures delay development. Females generally visit the nest twice every hour and brood the young for the first 7-12 days, after which time the nestlings can regulate their own body temperatures.

[*Chlorostilbon mellisugus*,
Ecuador.
Photo: F. Köster/Ardea]



Between days six and nine after hatching, there is an intermediate stage of development during which the main feather tracts grow but the dorsal down is retained. By this time, the eyes of these

Rufous-tailed

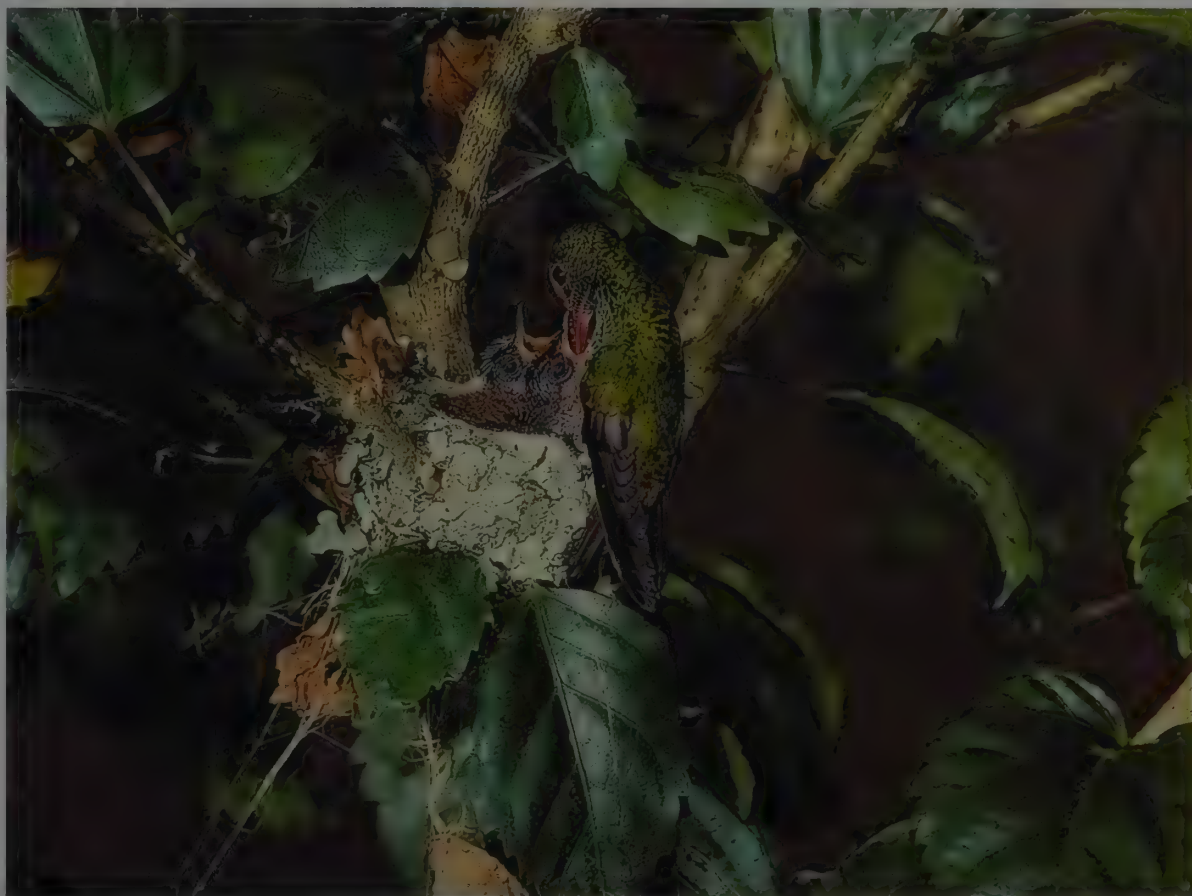
Hummingbird nestlings have opened and they sit more alertly in the nest. Although they no longer require direct touching to induce gaping, the feeding process is basically the same: the adult's bill is inserted deeply into the gape of her offspring before transference of food. Hummingbird chicks are fed frequently and grow rapidly, reaching almost 80% of their adult mass within 10-12 days.

This species is common in a broad variety of habitats including the edges of humid forest, coffee and banana plantations, scrub and gardens, ranging between sea-level and 1200 m from Costa Rica and Panama, south to western Ecuador.

Its relative success is at least partly explained by its generalist foraging strategy and its pugnacity. Individuals can feed on many different species of flowering plant, tolerating native and exotic species alike, while any hummingbird, *Hesperiidae* butterfly or euglossine bee that strays onto a territory is likely to be attacked in flight.

[*Amazilia tzacatl tzacatl*, Belize.]

Photo: Michael Gore]



on the head of the object of desire; similar effects can be achieved by presenting him or her with soap containing trochilid extracts. Evil spirits can be pacified by constructing a little altar with candles before the body of a hummingbird wrapped in red twine.

One of the traditional methods of capturing trochilids still in use is the employment of a long, flexible fishing rod-like tool, six or eight metres in length, with a blob of sticky lime at the end. This is carefully lowered on to the back of the bird as it hovers before a blossom, sticking it fast to the end of the rod. Native peoples have also used clay pellets shot from blowpipes to stun hummingbirds.

In the European and North American fashion markets, the breathtaking beauty of trochilid plumage quickly became a very desirable article. In the second half of the nineteenth century millions of hummingbird skins were exported from Central and South America, not only to decorate ladies' hats and clothes but also for the manufacture of feather pictures, ornaments, and artificial flowers. The collection of mounted specimens was promoted by the naturalist Adolphe Boucard as an interesting and appropriate hobby for ladies: "It is as beautiful and much more varied than a collection of precious stones, and costs much less....quite the thing for all those who have money, taste and leisure." In London in 1888, 12,000 trochilid skins were sold in one month; at one sale there 37,603 hummingbird skins from South America and Trinidad were auctioned; a single delivery from a Brazilian port contained 3000 Ruby Topaz skins; 152,000 hummingbirds were sold by one auction house in London between 1904 and 1911, and in 1905, some 8000 were used to make a single shawl. Already in 1851 E. J. Silva Maia of the National Museum in Rio de Janeiro was warning that some species had disappeared in the area purely as a result of trapping for the fashion industry. Some species were probably hunted to extinction in this slaughter since a few were first described from such skins but never subsequently seen, although the hybridization between species, and even genera, frequently reported for trochilids (see Systematics) would perhaps be responsible for some of these forms.

Ever since the first reports of brilliant, minute, nectar-feeding birds reached Europe in the sixteenth and seventeenth centuries people have wanted to be able to have them in captivity in order to study them closely, an activity virtually impossible in

their native habitats. In the year of the Great Exhibition, 1851, John Gould displayed 1500 mounted hummingbirds in the London Zoological Gardens, attracting 75,000 spectators, among them Queen Victoria. However, learning how to keep a bird with such unusual dietary requirements alive on the long journey across the Atlantic took some time. It was soon discovered that small insects or spiders had to be supplied along with the usual diluted honey or dissolved sugar. Both John Latham and Gould brought hummingbirds to England around the middle of the nineteenth century, but the birds died soon after arrival. In 1876, a collection of 50 trochilids belonging to six species could be seen in Paris, and two were admired in Hamburg three years later. The first hummingbird in London Zoo, a Sparkling Violet-ear, arrived in November 1905, but was dead fourteen days later. Trochilids drew huge crowds wherever they were shown, but no European zoo was able to emulate New York, where one bird remained alive for ten years. Eventually, the arrival of air transport put an end to the severe losses experienced in transit by ship.

A long process of trial and error has been necessary to arrive at the correct formula for artificial nectar, the best all-purpose liquid being a variable mixture of glucose, fructose and saccharose diluted in water to a concentration of around 10%. The protein element in the diet can be more problematic since it varies from species to species; lowland species are said to be "less sensitive" than those from uplands, which can quickly become ill on liquid protein supplements. Proteins obtained ultimately from mammals seem to give poorer results than those from hen's eggs or mashed mealworms, where a regular supply of live arthropods proves difficult. But finding the right balance is still a delicate business; too much remains unknown about the trochilid digestive system. Even zoos regard 5-10% of birds being alive after two years as a success, although private aviculturalists can sometimes achieve survival rates of around 50%. Captive birds can live on average for about ten years, and an age of 17 years has been recorded.

Learning the technique of breeding hummingbirds in captivity has taken even longer than discovering how to provide them with the diet they need. The first success in a zoological garden was in Cleveland, Ohio, with a Red-billed Streamertail pair in 1959, and in 1977 the same species was also the first to breed in a European zoo, at Wuppertal, Germany. About one-third of the roughly 80 species kept in captivity have attempted to breed but



These Blue-throated Goldentail chicks have entered the third stage of nestling development, which begins around day 10 and lasts until fledging. During this period, although their rectrices and remiges are still rather short, the chicks are almost completely feathered and they lose their dorsal down. By this time, they completely fill the tiny nest cup, which in this species has a characteristically incurved rim that expands slightly to accommodate them.

[*Hylocharis eliciae eliciae*, Costa Rica.
Photo: Michael & Patricia Fogden]



The Ruby-throated Hummingbird, and several other hummingbird species that visit the Nearctic to breed, exploit the superabundance of resources during the temperate summer, and then migrate, often long distances, to spend the winter in warmer, more southerly latitudes. These nestlings are almost fully grown and are nearly ready to leave the nest.

[*Archilochus colubris*, Illinois, USA.
Photo: Richard Day/
Oxford Scientific Films]

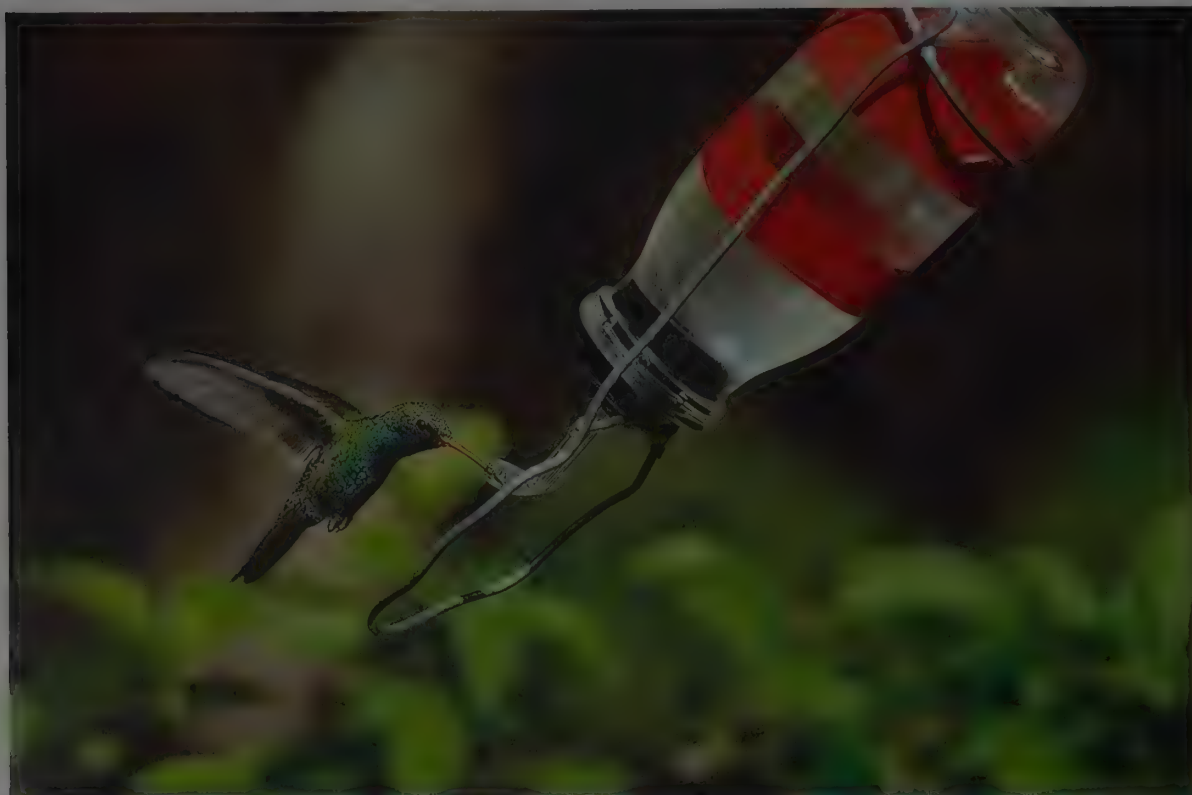
only around 20 have successfully done so worldwide since the 1950's. The birds' needs are best met in a large aviary with permanent water for bathing in the form of a shower, a fountain or soaking vegetation, while ample plant cover is also necessary for the hummingbirds to be able to conceal themselves in. A major difficulty in trying to encourage the birds to breed is that since they have no pair-bond they will not even attempt to breed unless they are able to execute their courtship displays. Another

problem often encountered is the well-known aggressive behaviour of trochilids; in the past, these pugnacious tendencies were countered by putting so many into one aviary that they were unable to hold territories, but it soon became clear that a few species would dominate the others, causing them physical harm and monopolizing the food sources. Another common mistake has been to keep some species in temperatures that were too high for them; upland species often require a cool environment. The

A few days before making their first flight, chicks become much more active, regularly perching on the side of the nest, preening and exercising their wings. Relatively few nestlings survive until fledging, this figure varying at around 20-40% for tropical species, while some high-altitude breeders such as the Andean genera *Oreotrochilus* and *Oxygogon*, and the Broad-tailed Hummingbird of the Rocky Mountains, have around 60% success rates. About 30% of nestling mortality in tropical hummingbirds is attributed to predation, and the immobility and silence of the nestlings of such species is clearly aimed at minimizing predation.



[*Selasphorus platycercus*, Wyoming, USA.
Photo: Jeff Foott/
BBC Natural History Unit]



The fact that hummingbirds will visit human habitations to sip artificially provided sugar solutions, as illustrated by this Broad-billed Hummingbird, has recently increased their popularity. Hummingbird feeding is popular in North America, and is becoming more so in the Neotropics. On the other hand, our admiration for them has occasionally led to a certain amount of persecution. Their iridescent plumage decorates the traditional ceremonial costume of tribal peoples, and was once extremely fashionable in Europe and North America. Birds are still trapped today to supply the avicultural trade.

[*Cyananthus latirostris magicus*, Arizona, USA.
Photo: Jeff Foott/Bruce Coleman]

ideal enclosure is thought to be a greenhouse full of plants with an adjoining open-air aviary. Disease can also cause high mortality, the commonest probably being mycosis, in particular various fungal infections of the respiratory passages.

Confronted with the task of describing hummingbirds, the ornithologist's first impulse on lifting the pen is often of a literary, almost poetic nature. Georges-Louis Leclerc, Comte de Buffon, the great eighteenth century naturalist, thought them "of all animated beings...the most elegant in form and brilliant in colour. The stones and metals polished by art are not comparable to this gem of nature. She has placed it in the order of birds, but among the tiniest of the race...she has loaded it with all the gifts of which she has only given other birds a share". A generation later John James Audubon described the hummingbird as a "glittering fragment of the rainbow...a lovely little creature moving on humming winglets through the air, suspended as if by magic in it, flitting from one flower to another, with motions as graceful as they are light and airy, pursuing its course and yielding new delights whenever it is seen". The final word should perhaps be left to one who was a poet before he was a birdman, the so-called Father of American Ornithology, Alexander Wilson, who was forced to leave his home in Paisley, Scotland, during the Napoleonic Wars, because of his revolutionary verses:

"What heavenly tints in mingling radiance fly!
Each rapid movement gives a different dye;
Like scales of burnished gold they dazzling show -
Now sink to shade, now like a furnace glow!"

Status and Conservation

Since 1987 all members of the Trochilidae have been placed on Appendix II of the Washington Convention on International Trade in Endangered Species (CITES). This means that their conservation status gives sufficient cause for concern that trade in live birds is regulated and is not allowed without a permit. In any case, virtually all countries with populations of trochilids have prohibited the export of live birds, so permit applications are rarely granted. Those birds most at risk are in Appendix I of the Convention, which forbids any trade at all involving them,

but at present the only hummingbird thus protected is the Hook-billed Hermit.

Although trochilids breed overwhelmingly in the Neotropics, a part of the globe where habitat destruction is widespread, intensive and continuous, most particularly in lowland rainforest where the giant trees preferred by loggers are easiest to extract, their situation is not as dramatically bad as that of many other Central and South American bird families. There are various reasons for this. Their nesting sites are generally in the lowest forest strata, and their minute nests can be built virtually anywhere where there is a large overhanging leaf, a cavity among tree roots, an overhang, or a low shrub. Also, where forest is cleared flowering plants may appear, albeit perhaps briefly, supplying the birds with adequate food, and even crop plantations like banana or coffee are not entirely hostile environments for some species. In addition, the relative paucity in lowland rainforest of those families of flowering plants preferred by trochilids, when compared to montane forest, shrubby habitats, ravines, *páramo* and other grasslands means that these lowland forests, in contrast to the Andes, have never been a stronghold of hummingbird diversity.

As an illustration, 163 trochilid species have been recorded in Ecuador, 135 in Colombia, and 100 in Peru, many species occurring in more than one of these countries, while Brazil, with an area of more than twice the total of these three countries together, supports a far more modest 84. The highest numbers of hummingbirds per unit area are found in the small Central American states.

An Endemic Bird Area is defined by BirdLife International as an area encompassing the overlapping breeding ranges of 2 or more restricted-range species such that their complete ranges fall inside its boundaries; restricted-range species are landbirds with a total natural breeding range estimated at less than 50,000 km². In their survey of the 20 countries in the world with the highest number of EBA's, eight are of vital importance for hummingbirds with four of them among the top five countries, the fifth being Indonesia. In all, there are 128 restricted-range trochilids, 39% of the 328 species recognized herein. The numbers of restricted-range trochilids in each of these eight countries, with the number of globally threatened hummingbird species endemic to each country in brackets, are: Colombia 37 (5); Peru 26 (4); Ecuador 22 (4); Venezuela 22 (3); Mexico 16 (4); Brazil 10 (1);

Hummingbirds have been less severely affected by deforestation than many other groups, partly because most species are not strictly reliant on primary forest. In fact, rainforest is unusually poor in hummingbird species due to the paucity of suitable flowering plants. They usually forage and nest in lower strata, tolerating fairly serious habitat degradation, indeed often actually benefiting from it, as clearings entail an increase in forest edge and flowering plants.

The Violet-chested Hummingbird occupies a restricted range in north-west Venezuela, but is not considered threatened as it survives well in secondary growth and plantations.

[*Sternoclyta cyanopectus*,
El Limón, Venezuela.
Photo: Luis Mazariegos]



Bolivia 7 (0); and Chile 2 (1). It should be noted that the sum of the restricted-range species appears greater than 128 since they may occur in more than one country. The total of globally threatened hummingbirds in these important EBA countries is 22, a very substantial fraction of the 27 classed as globally threatened throughout the Americas by BirdLife International; a further 22 species are placed in the Near-threatened category.

Of the 27 globally threatened hummingbirds, eight are classed as Critically Endangered, seven as Endangered, and twelve more as Vulnerable. However, one of BirdLife's eight Critically Endangered hummingbirds, the Bogota Sunangel, may not be a valid species or, if it is, may already be extinct. Equally, the so-called Tachira Emerald (*Amazilia Polyerata distans*), listed by BirdLife as Endangered, is almost certainly a hybrid between the Glittering-throated Emerald and the White-chinned Sapphire. Thus, for the present purposes, the numbers in these classes fall to seven and six respectively, and the total to 25. Population and status trends for birds like hummingbirds are more or less impossible to discern except over long time periods. Consequently between the first collation of all available information published in 1992 and the latest in 1998, only a very few species have been placed in different categories: the Hoary Puffleg has now been classed as Near-threatened rather than Vulnerable/Rare; the Neblina Metaltail is also now considered Near-threatened instead of Rare; and both the Tooth-billed and Beautiful Hummingbirds (*Calothorax pulcher*) have been removed from the Near-threatened category.

If we look at the situation of the seven trochilids in the Critically Endangered category more closely it should provide us with some case-studies of the various factors which, alone or especially in combination, can threaten the existence of a species.

The Hook-billed Hermit is now restricted to lowland Atlantic forests in eastern Brazil in the states of Bahia and Espírito Santo. There are estimated to be around 50-250 individuals remaining in highly fragmented and scattered remnants of the original habitat covering an area of perhaps less than 100 km²; its original range may once have been as large as 35,000 km². Its perilous situation is reflected by the fact that it is the only trochilid on Appendix I of CITES. This part of Brazil is densely populated and the influx of people continues unabated, so roads, settlements and agriculture, in the form of coffee, banana and rubber

plantations, are constantly eating into the forest. Other threats are logging and mining. Within the Brazilian part of the Atlantic Forest Lowlands EBA there are 51 Key Areas for birds, many of them with some sort of protected status, though resources are inadequate to implement conservation requirements. Illegal squatters, deliberately started or poorly controlled fires, road construction and so on continue to degrade protected areas, including even national parks. However the true status of this bird remains somewhat obscure, and additional hope for its future can be gained from the fact that five new bird species have been found in the general region in the last ten years, while others thought extinct have been rediscovered. Further exploration could conceivably reveal further populations of this hummingbird.



Of the 328 species of hummingbird currently recognized, some 128 (39%) occupy ranges estimated at less than 50,000 km². One of these is the Napo Sabrewing, a Near-threatened species which is apparently dependent on relatively intact forests in the Ecuadorian and Peruvian Andes. Like many hummingbirds it is very poorly known and until more data are collected detailing the habitat preferences, movements and threats of such species it is difficult to judge their conservation status accurately.

[*Campylopterus villaviscensio*,
Orito, Putumayo,
Colombia.
Photo: Luis Mazariegos]

The Sapphire-bellied Hummingbird is found only in and around small areas of mangrove forest on the north Colombian coast; all breeding individuals are apparently in a single population which could amount to less than 50 birds. Huge tracts of this rare habitat have been destroyed by urbanization and pollution which continue to threaten the remaining fragments. A new road and pipeline across the Isla de Salamanca National Park have altered tidal and river flows, leading to increased water salinity levels and the eradication of large areas of mangrove. This hummingbird species is severely threatened by a fatal combination of elements: a very small and probably declining population; a restricted habitat; and damaging human impact. Apart from the Isla de Salamanca National Park (21,000 ha), the hummingbird is protected within the Ciénaga Grande de Santa Marta Sanctuary (23,000 ha), but the areas of mangroves there have also suffered damage.

A hummingbird endemic to dry valleys in xeric scrub and thorn forest in the interior of northern Honduras is the Honduran Emerald (*Polyerata luciae*). It occurs at only a few locations and, although common at some of them, its range is extremely restricted and further population decline is likely. Until 1950 it was known from only 11 specimens but in 1988 it was found to be a common resident in the Aguán Valley. The principal threats are habitat destruction through the creation of pasture for cattle, pineapple plantations, and roads. The species can, however, tolerate a certain level of habitat alteration and has been observed feeding in heavily grazed understorey, but unless other populations are discovered it remains under very severe threat.

The Scissor-tailed Hummingbird (*Hylonympha macrocerca*) is endemic to the cloudforests of north-east Venezuela, occurring at around 1000 m. Although it is locally common, its entire range is encompassed by the Paria Peninsula National Park, the core area on the mountain of Cerro Humo being just around 15 km². Even within this nominally protected national park threats remain, chiefly in the form of agricultural encroachment, including burning to clear land, but also general human disturbance, road building, and so on. Once again the crucial combination of low numbers and a small, declining range has put this bird in the class Critically Endangered.

The Juan Fernandez Firecrown faces an even more complex series of threats. The species is restricted to the Juan Fernández

Islands in the south-eastern Pacific, 680-800 km west of Chile, an important centre of biodiversity; indeed, 98 of the 142 flowering plants recorded there are endemic to the islands. One race, *leyboldi*, is probably already extinct. It was confined to the island of Alejandro Selkirk (85 km²), and was last recorded in 1908, though some authorities hold that gene flow between the islands is likely and that the race may not have been valid anyway. The nominate race is present on the 93 km² island of Robinson Crusoe, where there are thought to be around 250-400 individuals. It is estimated that the entire population of the species in the archipelago in the nineteenth century could have been as high as 20,000 birds. The main conservation problems here are posed by introduced species, both plants and animals. Settlers have over the centuries brought with them dogs (now absent), cats, rats, mice, cattle, sheep, goats, rabbits and coatis (*Nasua nasua*). Only about 10% of the area of Robinson Crusoe retains its native vegetation of evergreen trees, tree ferns, ferns and the like. The Juan Fernandez Firecrown also faces competition from its congener, the Green-backed Firecrown, first noted on the larger island in 1830. The Green-backed copes much better with the non-native vegetation, since they are both of recent mainland origin, and there are now estimated to be around 5000 Green-backed Firecrowns on Robinson Crusoe. One of the principal threats from an introduced plant is posed by the bramble *Rubus ulmifolius*; apparently only the smaller female of the Juan Fernandez Firecrown, as well as both sexes of the Green-backed Firecrown, feed on its flowers. The islands have been a national park since 1935, a biosphere reserve since 1977, and have been nominated for the status of World Heritage Site. A US\$2,500,000 restoration programme by the Chilean government is at present under way; the survival of the Juan Fernandez Firecrown depends on its success.

The Black-breasted Puffleg (*Eriocnemis nigrivestis*) is found only in stunted elfin forest with páramo on mountain crests in north-west Ecuador, at altitudes of around 2500-4500 m, and is today possibly confined to a single peak, the volcano Pichincha, where three birds were seen in 1993, the first ones for 13 years. Its numbers in the past can be judged by the fact that over 100 skins can be found in museums. This puffleg is thought to be close to extinction, perhaps with a single population of below 50 birds, having declined because of habitat destruction for cattle



The Blossomcrown is endemic to Colombia, where it occupies a rather restricted range, within which it is generally rare, although locally abundant in parts of the Santa Marta Mountains. It occurs in humid forests and older stands of second growth, but is not known to tolerate major habitat degradation. It is not considered to be at immediate risk, but is classed as Near-threatened, implying that its status requires further investigation and monitoring.

[*Anthocephala floriceps floriceps*, Santa Marta, Colombia. Photo: Luis Mazariegos]



There is no evidence that the Hooded Visorbearer can withstand any degradation to its arid open-country habitat within its very small, entirely Brazilian, range. However, the remoteness and inhospitable nature of its favoured localities suggest that environmental damage, in the form of human population growth or agricultural expansion, is unlikely to be severe in the short term. It is thus currently treated as Near-threatened.

[*Augastes lumachella*,
Chapada Diamantina,
Bahia, Brazil.

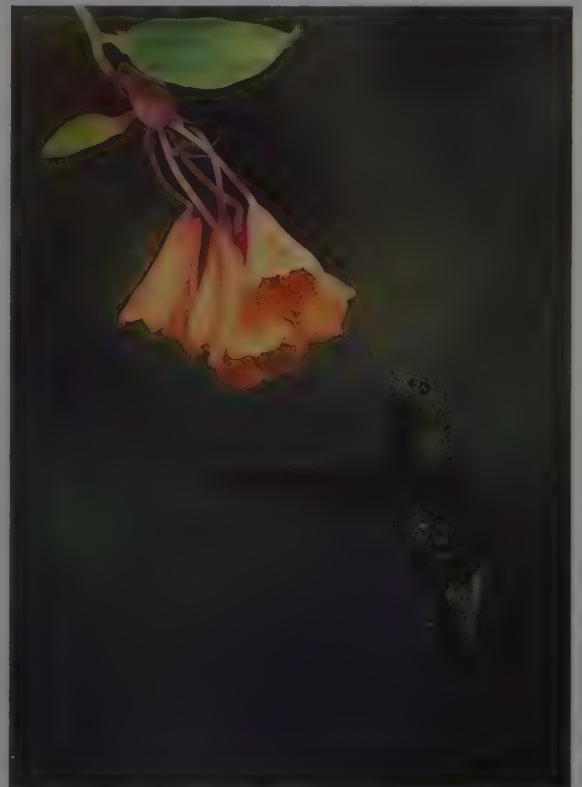
Photo: Luiz Claudio Marigo]

grazing, potato growing and charcoal making. However a concerted effort is being made by local and international conservationists to have its range protected. Since this is very close to the capital, Quito, much use is being made of press and television publicity. During the main part of the flowering season, in the rains between November and February, the Black-breasted Puffleg occurs at elevations of 3100-4500 m, when it most likely breeds in the humid elfin forest and *páramo*, spending the rest of the year in temperate forest at around 2400 m. This Critically Endangered hummingbird has one advantage in that it is apparently more of a generalist feeder than some others, and although its movements are particularly dependent on the flowering of *Fuchsia* and *Ericaceae* it seems that it will accept a wider range of food plants than was once thought. A crucial aspect of the threat facing the species is that it is an altitudinal migrant. This illustrates the important principle that it profits a montane species little if part of its range is declared a reserve while another habitat, upslope or downslope of the protected area and equally important for its survival, continues to be laid waste. For such birds a small protected area covering a large altitudinal range can be far more valuable than an extensive one spread over a single altitude. Ideally, similar considerations should also apply to long-distance migratory species to safeguard food supplies along the flyway between breeding and winter quarters.

The final hummingbird in the Critically Endangered category is another puffleg endemic to northern Ecuador, the Turquoise-throated Puffleg. It is known from a single locality in the arid ravine of the Río Guailabamba at 2100-2300 m in Pichincha Province, and could actually already be extinct. This locality is the only one named on the six museum skins in existence and is where the type specimen was taken in 1850. The forest of this area has been almost wholly cleared so unless new populations are found, perhaps in quite different habitats or even in southern Colombia, then the outlook for this species looks decidedly bleak.

If we briefly examine the reasons for placing some of the remaining 18 species in the IUCN categories Endangered and Vulnerable, the same overall pattern of threats emerges. All six of the species classed as Endangered occur in forest that is being cleared for cultivation, timber exploitation or settlements. Three of them are Mexican endemics, the Short-crested Coquette (*Lophornis brachylophus*), Oaxaca Hummingbird (*Eupherusa cyanophrys*) and

White-tailed Hummingbird (*Eupherusa poliocerca*), and all three inhabit the deciduous, semi-deciduous and montane evergreen forests and forest edges of the Sierra Madre del Sur EBA in the states of Guerrero and Oaxaca. This area is undergoing rapid deforestation, and the most pessimistic observers even suggest that it could be virtually cleared within the next few years. The low-altitude zones are being felled to make way for citrus fruits, maize and coffee, the cloudforest cleared for coffee plantations, while the oak,



The Black-thighed Puffleg is a poorly known species restricted to the Northern Central Andes EBA, where it is generally uncommon, occurring in humid forest borders and bushy pastures and preferring open vegetation. Given its small range and population, its survival would be of considerable concern if it relied on pristine habitats. However, it has adapted successfully to man-modified environments such as gardens and parks, and is therefore currently classed as Near-threatened.

[*Eriocnemis derbyi*,
Caldas, central Andes
of Colombia.

Photo: Luis Mazariegos]



Although previously considered Vulnerable, the Hoary Puffleg has been found to be more widespread than originally suspected. It is at least partially reliant on the presence of intact humid cloudforest along the Pacific slope of Colombia and Ecuador, and this habitat is rapidly disappearing. Nevertheless, healthy populations have been found in several protected areas such as La Planada Reserve in southern Colombia. After re-evaluation, its status has been adjusted to Near-threatened, although effective protection of relevant reserves remains vital.

[*Haplophaedia lugens*, La Planada Reserve, Nariño, Colombia.
Photo: Luis Mazariegos]

fir and pine trees above 1800 m are being taken as timber. Apparently only the White-tailed Hummingbird enjoys any degree of protection, since some of its range lies within Omiltemi State Ecological Park. This has an area of 96 km², while the entire EBA covers 12,000 km². All three of these trochilids are said to be locally common but have very restricted ranges, the Oaxaca Hummingbird in particular.

Another pair of sympatric Endangered congeners are the Little (*Chaetocercus bombus*) and Esmeraldas Woodstars (*Chaetocercus berlepschi*) of western Ecuador. They are found in one of the most threatened forest types in the Neotropics, namely moist evergreen forest. The Little has a much greater range than the Esmeraldas, extending into Peru, but there are few modern records of either species. The remaining hummingbird in this category, the Chestnut-bellied Hummingbird (*Amazilia castaneiventris*) from the eastern Andes of Colombia, is threatened as much by its small numbers as by habitat destruction. Rapid and extensive deforestation is widespread throughout the area, even inside sanctuaries, compounded by the apparent rarity of the species; there has been only a single record of the species in the last 30 years.

The threats faced by the twelve Vulnerable species vary little from the preceding cases. Forest habitat destruction poses the greatest risk to the survival of the majority of them. The Mexican Woodnymph (*Thalurania ridgwayi*), Black Inca (*Coeligena prunellei*), Royal Sunangel and Violet-throated Metaltail (*Metallura baroni*) are all considered locally common in parts of their ranges, but habitat fragmentation puts these populations under great pressure, and once below a critical level recovery is impossible without rigorous conservation measures. Protection is however rare and seldom effective. The Black Inca was once one of the most numerous of the so-called "Bogotá trade skins" but it is now restricted to a few cloudforest patches. Species perhaps less threatened by current habitat destruction than by critically small populations and/or restricted ranges, usually as a result of past human interference, are the Purple-backed Sunbeam (*Aglaeactis aliciae*), Colourful Puffleg, Grey-bellied Comet (*Taphrotesia griseiventris*), Marvellous Spatuletail, Chilean Woodstar and Glow-throated Hummingbird (*Selasphorus ardens*). The final two species in this class are the White-tailed Sabrewing (*Campylopterus curvipennis*) and the Mangrove Hummingbird. The population of the former on the island of Tobago

is still recovering from the devastation wrought by Hurricane Flora in 1963, thanks partly to an active conservation programme, an unusual instance of a hummingbird population put at risk by natural causes, though exacerbated by anthropogenic factors; the latter is severely threatened by clearance of mangroves on the Pacific coast of Costa Rica for salt-pans and shrimp ponds.

Only two of these 25 globally threatened hummingbirds do not at least partly inhabit forest or woodland of one type or an-



Few ecological data are available on the Pink-throated Brilliant, a restricted-range species of the foothills of the eastern Andes that seems to be uncommon and perhaps poorly adapted to utilize man-modified habitats. Humid forest within its range is still relatively extensive, but is under threat of clearance if current rates of destruction are maintained. The species is classed as Near-threatened, which highlights the importance of protecting areas of suitable habitat for this species and others largely or wholly restricted to the same area.

[*Heliodoxa gularis*, Serranía de los Churumbelos, Cauca, Colombia.
Photo: Luis Mazariegos]



The Colorful Puffleg is only known from wet subtropical forest in the vicinity of Chagwayaco, on the Pacific slope of the Andes in south-west Colombia. Like many other hummingbirds, its fate is ultimately tied to that of the forests it inhabits. With such a restricted range in an area where deforestation may be increasing, this species is classified as Vulnerable. Its future largely depends on the effective protection of the Munchique National Park, in which it has been found, and probably also the nearby Los Tambitos Nature Reserve.

[*Eriocnemis mirabilis*,
Cauca, Colombia.

Photo: Luis Mazariegos]

other: the Purple-backed Sunbeam, of scrub; and the Chilean Woodstar, of scrub, desert and agricultural areas. Indeed, of all 128 BirdLife International Restricted-range species, only nine are independent of forests. Many trochilids specializing in páramo grasslands, arid areas, scrubby thickets and so on face threats from habitat destruction for cattle raising or cultivation, but they possibly tend to be more adaptable, taking to secondary growth, plantations and gardens more readily than do true forest species. Those hummingbirds inhabiting high-altitude Andean páramo or puna and bordering stunted forest types, such as the hillstars (*Oreotrochilus*), the metalltails (*Metallura*) and the thornbills (*Chalcostigma*), face a lower risk because these rather inhospitable regions are in the main subject to relatively less human interference. The main threat in this zone is to the *Polylepis*-woodland ecosystem at around 3500-4500 m, as this is cleared to make way for subsistence cultivation and livestock, and there is much burning to create grazing; it is also plundered for firewood. However, of course, the primary factor affecting the family overall is that montane humid tropical and subtropical forests, the home of the majority of trochilids, continue to be destroyed at a hopelessly unsustainable rate.

The single hummingbird currently listed as Data-deficient, the Coppery Thorntail, has not been seen this century and is known solely from three nineteenth century museum specimens from Bolivia. It is probably the least known of all currently accepted trochilid species, although there is no argument over its status as a species; this seems destined to be an advantage of purely academic significance, as it is very possibly extinct already.

Only one hummingbird species is definitely known to be extinct, Brace's Emerald, from New Providence Island in the Bahamas. Although the taxon is known only from a single male taken in July 1877, it is quite likely to be a good species and not, as previously thought, a possible race of the Cuban Emerald (*Chlorostilbon ricordii*), also present in the islands though not on New Providence itself. Because the type locality was called into question all Bahaman *Chlorostilbon* were named *C. ricordii bracei*, until recent closer examination of the holotype, and the correspondence surrounding its collection, showed that the form should almost certainly be accorded species status. The collector himself shot two further individuals, both females, but he misidentified them and they were subsequently shown to be

Bahama Woodstars, providing an object lesson in the difficulties involved in attempting to ascertain the status of rare Trochilidae. Even when the holotype was taken the species must have been rare, and was probably restricted to scrubby thickets around the town of Nassau. No individual was ever seen again, but whether the cause of its extinction was primarily human interference or climate change remains obscure. Fossil remains appear to indicate that another trochilid no longer extant once inhabited New Providence.

The Bogota Sunangel was recently described from a single specimen bought in Bogotá in 1909, though properly examined only in the late 1940's, and it is thought to have come from the eastern or central Andes of Colombia, a region where much of the forest has been cleared for crops like potatoes, coffee and maize. It may still exist in the cloudforest at around 1400-2200 m, and would presumably be a relict species with a very restricted range. However, there is also the possibility that it could be a hybrid, in the same way that many of the Bogotá trade skins have proved to be. Some workers consider it to be a hybrid between Long-tailed Sylph (*Aglaiocercus kingi*) and the Fork-tailed Woodnymph, others that it is between the former and the Purple-backed Thornbill, or that one of the parents belonged to the genus *Heliangelus*. On the basis of this uncertainty the form is probably best not treated as a good species for the time being, although the case for its being so has certainly been well made. If it is a species and has disappeared it would be the first known extinction of a trochilid species in South America, though the great taxonomic uncertainty surrounding many forms known only from the odd trade skin leaves many questions in the air. Where the forests remain pristine there are still good hummingbird populations, showing that deforestation rather than nineteenth century collecting is responsible for the drastic reduction in range and numbers of many species.

The Trochilidae of North America provide some examples of low-level threats at present unlikely to have major effects on whole populations. The huge number of feeders placed by people in their gardens to attract hummingbirds can also have certain negative effects, doubtless outweighed, however, by the population and range increases that both feeders and garden flowers have made possible. The birds can come to depend on artificial feeding when food plants are not flowering, early or late in the season, and thus populations may be maintained at an un-



Only two of the 25 hummingbird species considered threatened do not inhabit forests at all. One of these is the Chilean Woodstar, a little-known species of scrub, desert and agricultural areas. Although these habitats are not immediately threatened, the species is treated as Vulnerable primarily because of its tiny range, in south Peru and north Chile. While it is probably relatively secure, its small populations are susceptible to collapse, and competition with the dominant Peruvian Sheartail (*Thaumastura cora*), a recent colonist, could prove detrimental to breeding and foraging success. It has usually been placed in monotypic *Eulidia*, but its morphology suggests it belongs in *Myrtis*.

[*Myrtis yarrellii*, Arica, northern Chile.
Photo: Luiz Claudio Marigo]

naturally high level. Sudden cold weather, disease (not uncommonly spread by contaminated feeders), monopoly of feeders by dominant species, predation by cats, and even hypothermia from too cold sugar-water taken while perched are all recorded causes of death, though no species is thereby threatened.

Birds such as Magnificent and Calliope Hummingbirds can be adversely affected by forest fires and tree-felling in their breeding range but this is generally a temporary setback. Conversely,

the forest clearings thereby created often provide perfect conditions for many of the food plants required by hummingbirds.

Probably the main conservation concern in North American trochilids centres on Costa's Hummingbird. The dry, scrubby places it inhabits in the south-western USA are threatened by residential development, and clearance for cattle grazing. Introduced South African buffelgrass grown for cattle is susceptible to fire, which destroys hummingbird food plants and nesting trees when it spreads

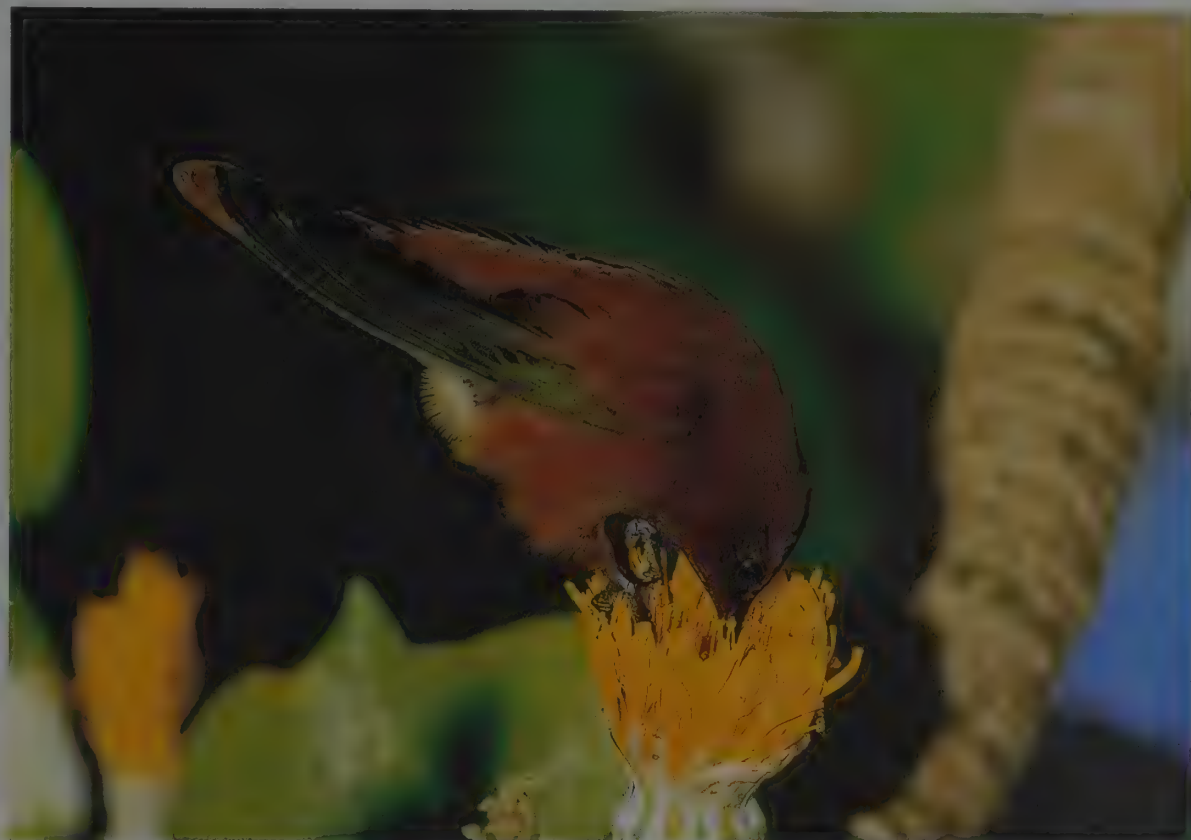


The rarely photographed Scissor-tailed Hummingbird is endemic to damp, mossy mid-altitude cloudforests of north-eastern Venezuela. Its range is very small and its habitat is disappearing rapidly, prompting its listing as Critically Endangered. The core area of suitable habitat on the Cerro Humo amounts to only 15 km². Even in this officially protected area within the Paria Peninsula National Park, agricultural encroachment and human disturbance are degrading the remaining forest. Note the marked sexual dimorphism.

[*Hylonympha macrocerca*, Cerro Humo, Paria Peninsula, Venezuela.
Left photo: Robert Clements.
Right photo: Josep del Hoyo/Lynx]

The Juan Fernandez Firecrown, endemic to its namesake islands in the south-eastern Pacific, is now restricted to a single island, where 250-400 birds are thought to survive. In comparison, 5000 individuals of its mainland relative, the Green-backed Firecrown (*Sephanoides sephanioides*), a recent colonist and competitor, also live on the island. Introduced cats, rats and coatis (*Nasua nasua*) have increased predation rates, while cattle, sheep, goats and rabbits have drastically altered the local environment, as have humans, so that only 10% of the island's area now retains native vegetation. A huge conservation programme aims to repair the island's devastated ecology, and the future of this Critically Endangered species depends on its outcome.

[*Sephanoides fernandensis*, Juan Fernández Islands, Chile.
Photo: Roland Seitre/Bios]



to the desert scrub. While fire in the species' other main habitat, chaparral, is part of a natural cycle and can benefit the bird, this is not so in the desert. Another threat faced by this species is that Anna's Hummingbird dominates at feeders and exotic garden plants in the new settlements built within its range.

Anna's Hummingbird has increased its range considerably since the 1930's, now reaching north up into British Columbia, when in the past the San Francisco area was its northern limit; it is also now found east to Arizona. Introduced plants like *Eucalyptus*, flowering when native ones do not, mean that the species remains in southern California after breeding instead of dispersing farther afield as before. Study areas with exotic flowering plants support 2-3 times more Anna's Hummingbirds than plots with only indigenous species.

The Ruby-throated Hummingbird has been shown to be absent within its nesting habitat in Nova Scotia where herbicides are used in forestry practice, apparently because of a lack of successional growth rather than poisoning. However, that this can endanger trochilids is reported from Brazil, where H. Sick described how hummingbirds "die by hundreds and thousands" in pineapple plantations due to excessive pesticide application.

Now that killing for plumage is firmly in the past, hummingbirds face no special threats directed specifically at them. They are difficult birds to keep and only relatively few specialists are interested in them for the aviary trade. Their fate is tied to that of countless other animal and plant species in the Neotropics, if rampant deforestation is allowed to continue at its current rate. The world will unquestionably be a poorer place if the tragic list of extinctions is to include more hummingbirds.

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Subfamily PHAETHORNITHINAE

Genus *RAMPHODON* Lesson, 1830

1. Saw-billed Hermit

Ramphodon naevius

French: Colibri tacheté German: Sägeschnabel-Schattenkolibri Spanish: Ermitaño Picosierra

Taxonomy. *Trochilus naevius* Dumont, 1818, Mount Corcovado, Rio de Janeiro, Brazil. Sometimes considered more closely related to genus *Androdon*, and placed in Trochilinae, but most morphological characters link it to hermits, in particular to genera *Eutoxeres*, *Glaucis* and *Threnetes*. Genus often considered to include *Glaucis dohrnii*. Description of race *freitasi* did not consider intraspecific variation related to age and sex. Monotypic.

Distribution. SE Brazil (S Minas Gerais and Espírito Santo to Santa Catarina; also recorded in Rio Grande do Sul).



Descriptive notes. 14-16 cm; 5.3-8.5 g. A large hummingbird; with *Eutoxeres*, one of the three heaviest hermits. Easily distinguishable from *Androdon aequatorialis*, the only other hummingbird with prominent saw-like serration of the mandibles, and, in adult male, a hooked tip to the upper mandible, by rufous-ochraceous throat with dark gular stripe. Bill almost straight. Male larger than female, with longer wings and tail, broader central rectrices and more contrasting coloration of underparts. Female has bill shorter, slightly decurved, and without hooked tip. Immature similar to adults, but with pale fringing to feathers of upperparts.

Habitat. Understorey of humid littoral forest up to 500 m.

Food and Feeding. Nectar of long-tubed flowers with steady-state blooming; recorded at *Justicia*, *Aechmea*, *Billbergia*, *Neoregelia*, *Nidularium*, *Quesnelia*, *Vriesea*, *Costus*, *Dahlstedtia*, *Erythrina*, *Nematanthus*, *Heliconia*, *Centropogon*, *Psychotria* and others. Small arthropods are mostly gleaned from vegetation. Like other hermit hummingbirds it is a trap-lining plant visitor, but it behaves aggressively over its feeding routes, excluding conspecifics as well as other hummingbirds.

Breeding. Gonadal activity indicates breeding Jul and Sept (São Paulo). Nest is loosely constructed, cone-shaped cup of plant material and cobwebs, attached to the underside tip of a long, pendent leaf. No further information.

Movements. No reliable information available. Presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Currently considered Near-threatened. Restricted-range species; present in Atlantic Forest Lowlands EBA. At least locally common, but habitat destruction may be a threat in future. Single record from Rio Grande do Sul, dating back to 1930.

Bibliography. Aleixo & Galetti (1997), Araujo *et al.* (1994), Belton (1984), Fischer (1994), Forrester (1993), Franco & Buzato (1992), Grantsau (1988), Guix *et al.* (1992), Hinkelmann & Schuchmann (1997), Hofling & Lencioni (1992), Oniki (1996), Pacheco (1997), Parker & Goerck (1997), do Rosário (1996), Ruschi (1978b, 1981-1982, 1986), Sazima *et al.* (1995), Scott & Brooke (1985), Selander (1966), Sick (1993, 1997), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Tobias *et al.* (1993), Vielliard (1994), Willis (1992), Willis & Oniki (1981).

Genus *EUTOXERES* Reichenbach, 1849

2. White-tipped Sickbill

Eutoxeres aquila

French: Bec-en-faucille aigle German: Weißkehl-Sichelschnabel Spanish: Picozoh Coliverde
Other common names: White/Bronze/Brown-tailed/Common Sickbill

Taxonomy. *Trochilus Aquila* Bourcier, 1847, Bogotá, Colombia.

Populations of E Panama and W Colombia sometimes separated as race *munda*, but morphological differences are based on a zone of character introgression between races *salvini* and *heterura*. Three subspecies normally recognized.

Subspecies and Distribution.

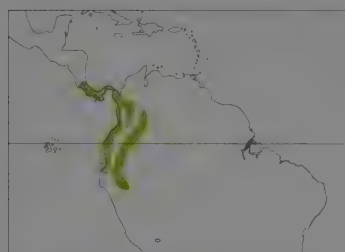
E. a. salvini Gould, 1868 - Costa Rica to W Colombia.

E. a. heterura Gould, 1868 - W Andes from SW Colombia to W Ecuador.

E. a. aquila (Bourcier, 1847) - E Andes from Colombia to N Peru.

Descriptive notes. 12-14 cm; male 10-12.5 g, female 8-10 g. Sickbills are unmistakable among all hummingbirds by their very strongly decurved bills. A large hermit hummingbird with dark green upperparts, dark green crown and nape, black and white streaked underparts, and dark (green and brown) rectrices with white tips. Female has shorter wing than male. Immature has light tips to remiges (mostly secondaries), and narrower rectrices than adult. Differences between races slight: nominate has the most prominent white tips to the rectrices and the most intensive orange-ochraceous edges to the undertail-coverts; adult male *heterura* has almost no white at the tips of the outer rectrices, and *salvini* tends to have lighter edging on undertail-coverts than other races.

Habitat. Understorey of humid and wet forest, older second growth, forest edge, near rivers, often in, or close to, *Heliconia* patches. Regularly between 300 and 700 m in Costa Rica, but recorded to sea-level as well as to 2100 m in Costa Rica and Colombia.



Food and Feeding. Nectar of *Heliconia* and *Centropogon* species with tubular blossoms similar in curved shape to bill, and small arthropods. Defends feeding flowers against other sickbills. Unlike most other hummingbirds, sickbills perch when feeding (recorded at *Heliconia* blossoms where this is possible).

Breeding. Jan-May in Costa Rica; data on gonadal condition indicate Mar and Jun in Panama, Aug in Colombia, Jun in Ecuador, and Sept in Peru. Nest is a loosely woven cup of plant materials (fibres, rootlets, etc.) attached by cobweb to the underside tip of a long, hanging leaf. 2 eggs; incubation 16-17 days, by female; chick black with grey down; fledging 22-25 days.

Movements. Sedentary; perhaps seasonal movements in some regions of Panama.

Status and Conservation. Not globally threatened. CITES II. Common throughout most of its range except the upper Magdalena Valley. Present in Braulio Carrillo National Park (Costa Rica); Río Nambi Reserve (S Colombia); and at Buenaventura (Piñas) and Tinalandia (Ecuador). In the lower Anchicaya Valley, near Buenaventura, SW Colombia, recorded density of at least 3-4 pairs/km².

Bibliography. Barnes *et al.* (1997), Blake (1989), Bloch *et al.* (1991), Fjeldsá & Krabbe (1990), Fogden (1993), Gill (1987), Hartert (1922), Hilty & Brown (1986), Hinkelmann (1985), Hinkelmann & Schuchmann (1997), Meyer de Schauensee (1949), Norton (1965), Remsen, Stiles & Scott (1986), Ridgely & Gwynne (1989), Ruschi (1961e, 1973b), Rutgers & Norris (1972), Salaman (1996), Slud (1964, 1980), Snow (1981), Stein (1992), Stiles (1975, 1979, 1980, 1985b, 1995b), Stiles & Skutch (1989), Stotz *et al.* (1996), Vigle (1982), Wetmore (1968a), Williams & Tobias (1994), Zimmer (1950b).

3. Buff-tailed Sickbill

Eutoxeres condamini

French: Bec-en-faucille de La Condamine

Spanish: Picozoh Colicanela

German: Rotschwanz-Sichelschnabel

Other common names: Rufous-tailed Sickbill

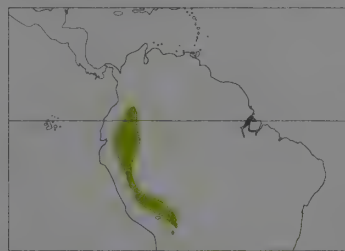
Taxonomy. *Trochilus Condamini* Bourcier, 1851, Archidona, Ecuador.

Races not well-separated geographically, forming a character introgression zone in N Peru. Taxonomic treatment of southernmost populations is under review. Two subspecies recognized.

Subspecies and Distribution.

E. c. condamini (Bourcier, 1851) - E Andes from SE Colombia to N Peru.

E. c. gracilis Berlepsch & Stolzmann, 1902 - E Andes of Peru and NW Bolivia.



Descriptive notes. 13-15 cm; male 10-12.5 g, female 8-10 g. A large hermit hummingbird, similar to *E. aquila* but with buffish outer tail feathers with white tips, blue patches on both sides of nape, and, in adult, mid-crown stripe bare of feathers. Female has shorter wings than male. Immature has light tips to remiges (mostly secondaries), narrower rectrices than adult, smaller blue nape patch and lacks unfeathered central line on the crown. Birds of race *gracilis* have shorter bill, and less distinct tailward extended belly streaking.

Habitat. Similar to *E. aquila*, but, particularly where common, from SE Colombia to N Peru.

more often in open, cultivated, or disturbed areas such as plantations, mossy forest, swamp forest, wooded ravines, near streams as well as in bamboo. Recorded between 180 and 3300 m in Peru.

Food and Feeding. Nectar (recorded at flowers of *Heliconia* and *Centropogon*) and small arthropods. Feeding by trap-lining confirmed, although presumably "feeding flowers as well."

Breeding. Season undetermined, but data on gonadal activity indicate Sept-Nov in Peru. Nest similar to that of *E. aquila*. 2 eggs; incubation 16-18 days, by female; chick black with grey down; fledging 22-24 days. First breeding in second year.

Movements. No reliable information available, presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Locally common along ravines and rivers with semi-open secondary growth and *Heliconia* stands. Very abundant in disturbed Andean foothills of the Rio Napo area of E Ecuador, with density of at least 3-5 pairs/km² recorded.

Bibliography. Best *et al.* (1997), Butler (1979), Cardiff & Remsen (1981a), Fjeldsá & Krabbe (1990), González (1998), Hilty & Brown (1986), Hinkelmann (1985), Hinkelmann & Schuchmann (1997), Meyer de Schauensee (1949), Norton (1965), Parker *et al.* (1982), Remsen & T aylor (1989), Remsen, Stiles & Scott (1986), Rutgers & Norris (1972), Salaman & Mazariegos (1998b), Snow (1981), Stotz *et al.* (1996), Terborgh *et al.* (1984), Zimmer (1930, 1950b).

Genus *GLAUCIS* Boie, 1831

4. Hook-billed Hermit

Glaucis dohrnii

French: Colibri de Dohrn

Spanish: Ermitaño de Espíritu Santo

German: Bronzeschwanz-Schattenkolibri

Taxonomy. *Trochilus dohrnii* Bourcier and Mulsant, 1852, Ecuador; error = Rio de Janeiro.

On following pages: 5. Hairy Hermit (*Glaucis hirsuta*); 6. Bronzy Hermit (*Glaucis aenea*); 7. Band-tailed Barbthroat (*Threnetes ruckeri*); 8. Pale-tailed Barbthroat (*Threnetes niger*); 9. Broad-tipped Hermit (*Anopetia gouellei*); 10. White-whiskered Hermit (*Phaethornis yaruqui*); 11. Green Hermit (*Phaethornis guy*); 12. White-bearded Hermit (*Phaethornis hispidus*); 13. Western Long-tailed Hermit (*Phaethornis longirostris*); 14. Eastern Long-tailed Hermit (*Phaethornis superciliosus*).

Often considered to belong to genus *Ramphodon*, but morphological characters clearly indicate placement in *Glaucis*. Monotypic.

Distribution. SE Brazil (Bahia and Espírito Santo).



Descriptive notes. c. 12-13 cm; male 6-8 g, female 5.5-7 g. A medium-sized hermit hummingbird similar to female *G. hirsuta*, i.e. with uniform ochraceous orange underparts, though with an almost straight bill and no rufous tail coloration. Adult male with some serration on edge of both mandibles. Female has shorter, more curved bill, shorter wings, narrower central rectrices, and is somewhat paler than male. Immature undescribed.

Habitat. Understorey of lowland (below 500 m) primary forest, littoral forest, mainly in damp areas along streams, particularly in areas with abundant *Heliconia* plants.

Food and Feeding. Nectar and small arthropods. Rare observations indicate feeding at same flowers as *G. hirsuta*. Feeds by trap-lining.

Breeding. Sept to Feb. Available information points to a nest construction similar to *Ramphodon naevius* or *G. hirsuta*. 2 eggs; incubation at least 15 days, by female; fledging 20-27 days.

Movements. No precise information available. Presumably sedentary, although sparsity of records at particular sites might reflect movements of some sort.

Status and Conservation. CRITICALLY ENDANGERED. CITES I. Restricted-range species: present in Atlantic Forest Lowlands EBA. Has declined greatly due to habitat loss, with overall range now reduced from perhaps c. 35,000 km² to possibly under 100 km²; total numbers now estimated at only c. 50-250 birds. Occurs at only a few widely scattered localities, possibly now only Porto Seguro Reserve and Pau Brasil Ecological Station in Bahia, and Linhares Reserve in Espírito Santo; at the last of these, only a single recent record despite presence of many observers; Córrego Grande Federal Biological Reserve (Espírito Santo) formerly thought to be a stronghold of the species, but now almost certainly extinct there. Nevertheless, true status remains uncertain, and further populations of the species might still survive. Main problem is continuing encroachment on habitat for settlement, mining and logging, with concomitant agriculture, fires and road building. See page 529.

Bibliography. Bernardes *et al.* (1990), Collar (1987), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Gonzaga *et al.* (1987, 1988), Grantsau (1988), Hinkelmann & Schuchmann (1997), King (1978/79), Knox & Walters (1994), Oniki (1996), Pinto (1935), Ruschi (1961g, 1965d, 1967b, 1969, 1974, 1976b, 1981-1982, 1982a, 1986), Sargeant (1996), Sick (1969, 1972, 1993, 1997), Sick & Teixeira (1979), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Wege & Long (1995).

5. Hairy Hermit

Glaucis hirsuta

French: Ermite hirsute **German:** Rotschwanz-Schattenkolibri **Spanish:** Ermitaño Hirsuto
Other common names: Rufous-breasted Hermit

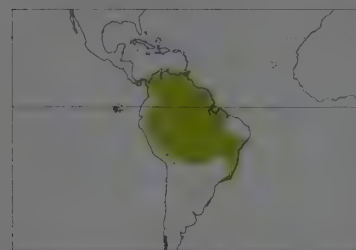
Taxonomy. *Trochilus hirsutus* J. F. Gmelin, 1788, north-eastern Brazil.

Sister species of *G. aenea*, and these two often considered conspecific, but they meet in W Panama and W Colombia without interbreeding; present species interrupts former probably continuous distribution of *G. aenea* and presumably in gradual process of replacing it. Several attempts have been made to subdivide present species into races, with *affinis* of the Guianas, *mazeppa* of CE Brazil, and *abrawaya* of SE Brazil; these were based on plumage differences in immature and adult males and females, but did not take into consideration intraspecific variation in coloration and measurements independent of geography; only birds from Grenada, Trinidad and Tobago are morphologically separable. Includes "*Threnetes grizeki*", based on immature male plumage. Two subspecies currently recognized.

Subspecies and Distribution.

G. h. insularum Hellmayr & von Seilern-Aspang, 1913 - Grenada, Trinidad and Tobago.

G. h. hirsuta (J. F. Gmelin, 1788) - Panama, Colombia W of the Andes, and E of the Andes S to C Bolivia, and through Venezuela to the Guianas and almost all of Brazil.



Descriptive notes. 10-12 cm; male 6-8 g, female 5.5-7.5 g. A medium-sized hermit with dark green upperparts, brownish-rufous underparts, slightly decurved bill and the four outer rectrices rufous with broad black subterminal bands and white tips. Female has distinctly paler throat and upper breast; shorter wings and tail; narrower rectrices; bill more decurved. Male has serrated edges on both mandibles, female only on upper mandible; male sometimes has a somewhat hooked tip to upper mandible. Immature has feathers of upperparts ochraceous, and pale tips to remiges; narrower rectrices; immature male

has some prominent dark throat feathers resembling throat coloration in *Threnetes*. Race *insularum* has significantly longer wings and more decurved bill.

Habitat. Understorey of many types of forest and dense vegetation outside primary forest: second growth, woodland clearings, disturbed and secondary forest, riverine habitats, swamps, shrubs, forest edge, partly deciduous forest, bamboo thickets, gallery forest, islands of trees or shrub in grassland, *cerrado* and plantations. Recorded from sea-level to 1800 m, though mostly below 1000 m; possibly up to 3500 m in Venezuela.

Food and Feeding. Nectar of *Heliconia*, *Centropogon*, *Pachystachys*, *Passiflora*, *Trichanthera* and *Costus* species, as well as small arthropods.

Breeding. Jan-Jul on Trinidad, Apr-Jul in Panama. Sept-May in Brazil. Nest records in Sept in SE Colombia; Dec and May in N Colombia; Jun in E Colombia; Sept, Nov and Dec in Surinam; Feb, Mar, Jul, Aug and Dec in French Guiana. Data on gonadal activity indicate Feb in Venezuela; Feb and Jun in Colombia; Aug in Panama; Jan, Aug and Sept in Peru; Aug-Sept in Brazil. Nest built on underside of pendant leaf, a cone-shaped cup loosely constructed of plant strands decorated with lichens and plant matter, similar to nests of *Ramphodon naevius* and *Eutoxeres*; eggs partly visible from the outside. In contrast to most other hummingbirds, males recorded in immediate nest area, and reported to defend nest. Normally 2 eggs; higher clutch sizes are due to conspecific females laying in the same nest. Incubation 17-19 days, by female; chick black with grey down; fledging 20-25 days; young remain with female for 3-4 weeks. First breeding in second year.

Movements. No reliable information available. Presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Generally common throughout much of its extensive range, especially in Amazonia; the most commonly netted hummingbird species at Amacayacu National Park (SE Colombia). Occurs in Guatopo National Park (Venezuela) and Asa Wright Nature Centre (Trinidad). Appears to have declined in some areas due to degradation or destruction of forest, with extensive loss of its main food plants, e.g. in Henri Pittier National Park in NW Venezuela.

Bibliography. Belton (1984), Bond & Meyer de Schauensee (1943), Cintra & Yamashita (1990), Cotton (1998a), Davis, S.E. (1993), Davis, T.J. *et al.* (1991), Dubs (1992), Feinsinger *et al.* (1982), ffrench (1991), Fjeldså & Krabbe (1990), Friedmann (1948), Grantsau (1988), Gyldenstolpe (1945b), Haffer (1975), Haverschmidt (1968), Haverschmidt & Mees (1994), Hayes & Samad (1998), Hilty & Brown (1986), Hinkelmann (1988b), Hinkelmann & Schuchmann (1997), King (1978/79), Mayr & Vuilleumier (1983), Meyer de Schauensee & Phelps (1978), Novaes & de Carvalho (1957), Olson (1993), Oniki (1996), Oniki & Willis (1983), Pinto (1953), Prestel (1985), Raffaele *et al.* (1998), Remsen & Parker (1983), Remsen, Stiles & Scott (1986), Ridgely & Gwynne (1989), do Rosário (1996), Rosenberg, G.H. (1990), Ruschi (1973c, 1973d, 1973e, 1976b, 1981-1982, 1982a, 1986), Rutgers & Norris (1972), Sazima *et al.* (1995), Schäfer & Phelps (1954), Schuchmann (1977a), Sick (1993, 1997), Sneath (1935), Snow, B.K. (1973a), Snow, B.K. & Snow (1972), Snow, D.W. & Snow (1964, 1973), Stotz *et al.* (1996), Terborgh *et al.* (1984), Thomas (1993), Todd & Carriker (1922), Tostain *et al.* (1992), Vuilleumier & Mayr (1987), Wetmore (1968a), Worth (1942).

6. Bronzy Hermit

Glaucis aenea

French: Ermite bronzé **German:** Kupferschattenkolibri **Spanish:** Ermitaño Bronceado
Other common names: Bronze/Chestnut-colored Hermit

Taxonomy. *Glaucis aeneus* Lawrence, 1867, Costa Rica.

Sister species of *G. hirsuta*, and these two often considered conspecific, but they meet in W Panama and W Colombia without interbreeding; present species probably had continuous distribution in past, but now interrupted by *G. hirsuta*, by which it is presumably being gradually replaced. Slight size and weight differences exist between the two discrete populations. Central American birds having longer wings than South American ones, but plumage coloration identical; South American populations sometimes separated as *race cubiana*. Monotypic.

Distribution. E Honduras, E Nicaragua and Costa Rica to W Panama; W Colombia to W Ecuador.



Descriptive notes. 9-10 cm; male 3-6 g, female 3-6 g. Very similar to, but smaller than *G. hirsuta*, with, in general, slightly more decurved bill in both sexes, and upperparts of a regular bronzy or coppery-green colour. Male has throat and upper breast like belly; serrated edges found only on adult male upper mandible. Female has slightly shorter wings than male and more decurved bill with no serration. Immature similar in coloration to that of *G. hirsuta*.

Habitat. Disturbed primary forest, dense or old second growth, forest borders, thickets and shrubbery, swamp forest, near streams. Recorded to 750 m in Costa Rica and 800 m in Colombia.

Food and Feeding. Nectar, e.g. of *Heliconia* species; also small arthropods.

Breeding. May-Aug in Colombia, Jan-Aug in Costa Rica, nest records in Jun, Jul in W Panama, gonadal data also indicate Mar and Apr in Colombia. Nest similar to that of *G. hirsuta*. 2 eggs; development of young similar to *G. hirsuta*.

Movements. Presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Very common along the Pacific coast of the Chocó region. In the lower Anchicayá Valley, near Buenaventura, SW Colombia, density of at least 2-4 pairs/km² recorded. Recently recorded for first time in Honduras, in catchment area of Río Plátano, where was found to be one of commonest hummingbird species in *Heliconia* thickets. In Pacific lowlands of Costa Rica, present in Corcovado National Park, Carara Biological Reserve and Golfo National Wildlife Refuge. In Ecuador, occurs in Río Palenque Science Centre (S of Santo Domingo).

Bibliography. Anderson *et al.* (1998), Blake & Loiselle (1991), Hilty & Brown (1986), Hinkelmann & Schuchmann (1997), Olson (1993), Prestel (1985), Remsen, Stiles & Scott (1986), Ridgely & Gwynne (1989), Salaman & Mazariegos (1998b), Skutch (1972), Slud (1964), Stiles (1975, 1979, 1980, 1995a, 1995b), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968a), Worth (1939, 1942).

Genus THRENETES Gould, 1852

7. Band-tailed Barbthroat

Threnetes ruckeri

French: Ermite de Rucker **Spanish:** Ermitaño Barbudo Colibandeado
German: Weißbinden-Schattenkolibri

Other common names: Rucker's Hermit, Rucker's/Blue Fan-tailed Barbthroat

Taxonomy. *Trochilus Ruckeri* Bourcier, 1847, Esmeraldas, Ecuador.

Proposed race *darienensis* based on birds from an extensive zone of character introgression in E Panama and N Colombia, involving *ventosus*, nominate and *venezuelensis*. Three subspecies currently recognized.

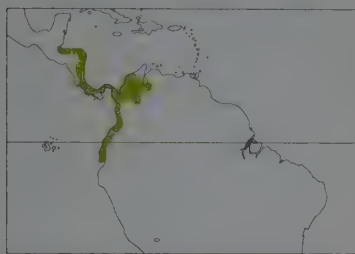
Subspecies and Distribution.

T. r. ventosus Bangs & Penard, 1924 - E Guatemala and Belize to Panama.

T. r. ruckeri (Bourcier, 1847) - N & W Colombia and W Ecuador.

T. r. venezuelensis Cory, 1913 - NW Venezuela.

Descriptive notes. 10-11 cm; male 5.5-7 g, female 5-7 g. A medium-sized hermit with contrasting underpart coloration, almost straight bill, and dark tail feathers with white tips; prominent white base to outer tail feathers, creating broad subterminal black band. Male has more clearly contrast-



open shrubbery, thickets, plantations, near rivers. Recorded from sea-level to 1200 m.

Food and Feeding. Nectar of *Heliconia*, *Costus* and other tubular flowers; also small arthropods, especially spiders. Feeds by trap-lining. Nectar robbery recorded by regular piercing of *Calathea*, some *Heliconia* species, and other tubular blossoms too long for its bill.

Breeding. Feb-May in Costa Rica, Caribbean slope; Jun-Sept in Costa Rica, Pacific slope; nesting recorded May in Honduras, and Dec in Costa Rica; data on gonadal condition indicate Jun in Panama, Jul in Honduras, Jan-Apr and Sept in Colombia. Nest is a more or less loosely built cup of rootlets, plant fibres, vegetable hairs and cobweb, denser than that of *Glaucis*, fixed at the underside tip of a long, pendent leaf. 2 eggs; incubation 15-18 days, by female; fledging 23-25 days; young remain with female for 3-4 weeks. Male observed in the vicinity of an incubating female.

Movements. Presumably sedentary, although some post-breeding movement recorded, in particular of young birds.

Status and Conservation. Not globally threatened. CITES II. Common along forest borders of Pacific slopes of Colombia and NW Ecuador. In foothills of Tumbaco (SW Colombia) density of at least 3-6 pairs/km² recorded; at Río Santiago (NW Ecuador) at least 2-3 pairs/km². In Pacific lowlands of Costa Rica, present in Corcovado National Park, Carara Biological Reserve and Golfito National Wildlife Refuge; in Ecuador, at Tinalandia and Río Palenque Science Centre.

Bibliography. Barlow *et al.* (1972), Blake (1989), Gill (1987), Harms & Ahumada (1992), Hilty (1997), Hilty & Brown (1986), Hinkelmann & Schuchmann (1997), Howell & Webb (1995a), Howell *et al.* (1992), Land & Kiff (1965), Meyer de Schauensee & Phelps (1978), Monroe (1968), Pople *et al.* (1997), Remsen, Stiles & Scott (1986), Ridgely & Gwynne (1989), Robbins & Ridgely (1990), Skutch (1964a, 1972), Slud (1964), Stiles (1979, 1980, 1985b, 1995b), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968a), Wood & Leberman (1987).

8. Pale-tailed Barbthroat

Threnetes niger

French: Ermite à queue blanche

German: Orangekehl-Schattenkolibri

Spanish: Ermitaño Barbudo Común

Other common names: White-tailed Barbthroat (*leucurus*); Bronze-tailed Barbthroat (*loehkeni*); Sooty Barbthroat (*niger*); Christina's Barbthroat ("christina")

Taxonomy. *Trochilus niger* Linnaeus, 1758. Cayenne.

Species long known as *T. leucurus*, but taxon *niger*, traditionally considered a separate species, represents a melanistic form of geographically limited distribution, based on apomorphic characters within the range of variation found in *leucurus*; otherwise the two are apparently inseparable, so conspecific treatment seems appropriate, with older name *niger* claiming priority. Since there are several regions from which no or only a few specimens have been secured, exact limits of racial distributions not yet reliably determined. Race *loehkeni* sometimes regarded as separate species; appears to be intermediate between *leucurus* and *niger*; proposed race *freirei* from Amapá (N Brazil) is inseparable from a dull male *loehkeni* and may confirm the intermediate position of latter; both *niger* and *loehkeni* are very rare in scientific collections. In W Amazonia, two zones of character intergradation exist between races *cervinicauda* and *rufigastera* on the one hand, and *leucurus* and *rufigastera* on the other, apparent in belly and tail coloration. Proposed race *cristinae* is synonym of *loehkeni*. Six subspecies currently recognized.

Subspecies and Distribution.

T. n. cervinicauda Gould, 1855 - E Colombia to N Peru and adjacent W Amazonian Brazil.

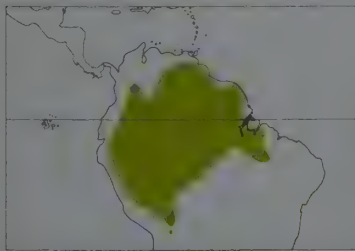
T. n. rufigastera Cory, 1915 - C Peru to N Bolivia.

T. n. leucurus (Linnaeus, 1766) - S Venezuela, Guyana and Surinam through Amazonian Brazil to N Bolivia.

T. n. niger (Linnaeus, 1758) - French Guiana and adjacent Brazil (N Amapá).

T. n. loehkeni Grantsau, 1969 - NE Brazil N of Amazon (Amapá).

T. n. medianus Hellmayr, 1929 - NE Brazil S of Amazon (Pará).



tips to remiges; in subspecies with light tail feather markings, these are more extensive in adult birds. Racial differences based on colour of belly and the four outer pairs of tail feathers: nominate has uniform dark brownish grey underparts with some lighter shading, where all other races have a bright orange throat; races *cervinicauda* and *medianus* agree in light grey-ochraceous belly coloration, but have light ochraceous (*cervinicauda*) or pastel-coloured (in *medianus* even lighter and brighter ochraceous) tail markings, whereas *loehkeni* differs by uniform dark tail feathers with only some light coloration at tips; *leucurus* has greyish belly and white outer rectrices with some dark only near tips; *rufigastera* has rufous ochraceous belly and white tail feathers as *leucurus*.

Habitat. More open places in humid lowland and higher-altitude tropical forest, river edge forest, transitional and swamp forest, second growth, brushy pastures, plantations. Nominant race often found in riverine habitats, with *Lechnocypus* as characteristic plant. Occurs below 500 m in French Guiana, recorded from sea-level to 1500 m in Peru, to 1600 m in Ecuador.

ing throat, breast and belly, with some iridescent green feathers even on the underparts. Female has shorter wings and tail, and more decurved bill than male. Immature differs by ochraceous feather edges on upperparts and light tips to remiges. Racial differences slight: nominate has smallest extent of pale ochraceous throat coloration, *venezuelensis* more so, but less than *ventosus*, which has extensive bright orange throat and more ochraceous belly than other races; both *ruckeri* and *venezuelensis* have grey bellies.

Habitat. Understorey of primary and disturbed forest, forest edge, dense second growth, semi-

Food and Feeding. Nectar of *Heliconia*, *Costus*, *Monotagma* and other flowering species, as well as small arthropods. Feeds by trap-lining.

Breeding. Nov-Feb, with additional nests recorded May, Sept and Oct in NE Brazil S of Amazon; Jan-Mar in Guyana; data on gonadal activity indicate Jul-Oct in Pará, Brazil; Aug-Nov in Peru; Feb in Ecuador. Nest similar to *Ramphodon naevius* or *Glaucis hirsuta*, but more densely constructed, with more lichens in external wall. 2 eggs; incubation 16-18 days, by female; chick has dusky pinkish skin and dusky down; fledging c. 23-24 days.

Movements. Presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Local and uncommon throughout distribution range. Regularly seen at the Voltzberg area in Surinam; in French Guiana, present at Saint Georges, Saint Elie and Saul; also occurs in Tambopata Reserve (Peru) and Imataca Forest Reserve (Venezuela). Status and precise distribution of races *niger* and *loehkeni* insufficiently known.

Bibliography. Bond & Meyer de Schauensee (1943), Bloch *et al.* (1991), Cotton (1998a), Davis *et al.* (1991), Dyre (1990), Friedmann (1948), Grantsau (1969, 1988), Gyldenstolpe (1945b), Haverschmidt & Mees (1994), Hilty & Brown (1986), Hinkelmann (1988b), Hinkelmann & Schuchmann (1997), Mayr & Vuilleumier (1983), Meyer de Schauensee & Phelps (1978), Novas (1974), Oniki & Willis (1983), Pacheco (1997), Peres & Whittaker (1991), Remsen & Parker (1983), Remsen, Stiles & Scott (1986), Ruschi (1957a, 1975b, 1976c, 1981-1982, 1986), Sick (1993, 1997), Skutch (1972), Sneath (1935), Snow (1973b, 1981), Stotz *et al.* (1996), Terborgh *et al.* (1984), Tostain *et al.* (1992), Viellard (1994), Vuilleumier & Mayr (1987), Williams & Tobias (1994), Zimmer (1950a).

Genus ANOPETIA Simon, 1918

9. Broad-tipped Hermit

Anopetia gounellei

French: Ermite de Gounelle German: Caatingaschattenkolibri Spanish: Ermitaño Coliancho

Taxonomy. *Phaethornis* [sic] *gounellei* Boucard, 1891, San Antonio da Barra, Bahia, Brazil.

Often placed in genus *Phaethornis*, but different bill and tail morphology support treatment in a separate genus. Monotypic.

Distribution. E Brazil (Piauí to Bahia).



Descriptive notes. c. 11 cm; about 3 g in both sexes. A small hermit hummingbird with bronzy-green upperparts, light brownish to ochraceous underparts, and dark brown throat edged orange-ochraceous. Upper mandible base broadened on both edges thus covering base of lower mandible. Differs from *Phaethornis* in that central pair of rectrices is of similar length as second, or next pair, with larger white tips. Male has broader central rectrices than female, but no obvious differences in tail length and bill curvature; female perhaps has shorter wing than male. Immature birds undescribed.

Habitat. Caatinga region where inhabits more humid areas with shrubs or trees and dense undergrowth; arboreal, shrubby and secondary caatinga. Semi-deciduous forest in the adjacent campo cerrado (S Bahia). Recorded between 500 and 700 m.

Food and Feeding. Nectar and small arthropods. Presumably trap-lining feeding behaviour.

Breeding. Incubation said to be 14 days, fledging up to 20 days. No further information.

Movements. No information available, but presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Poorly known and might perhaps be classed as Data-deficient. Presumably uncommon in general, although regularly seen; occurs in a relatively unthreatened habitat. In Bahia, regularly recorded in caatinga W of Boa Nova, and also around Canudos. Very rare in scientific collections.

Bibliography. Forrester (1993), Gounelle (1909), Grantsau (1988), Hinkelmann & Schuchmann (1997), Meyer de Schauensee (1982), Olmos (1993), Ruschi (1986), Sargeant (1996), Sick (1993, 1997), Sneath (1928a), Stotz *et al.* (1996), Tobias *et al.* (1993), Willis (1992).

Genus PHAETHORNIS Swainson, 1827

10. White-whiskered Hermit

Phaethornis yaruqui

French: Ermite yaruqui German: Smaragdschattenkolibri Spanish: Ermitaño de Yaruqui

Other common names: Black-winged/Yaruquian Hermit

Taxonomy. *Trochilus Yaruqui* Bourcier, 1851, Yaruqui, Ecuador.

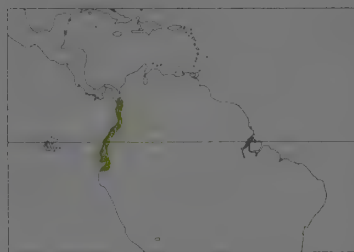
W Colombian populations formerly separated as race *sanctijohannis*, but description was based on immature birds. Monotypic.

Distribution. W Colombia and W Ecuador; possibly SW Panama.

Descriptive notes. c. 13 cm; male 4-7 g, female 4-6.5 g. Medium-sized hermit hummingbird with bluish green upperparts, green to dark grey underparts, and white gular stripe which may be reduced almost to invisibility in older birds. Adult bird has more iridescence in plumage than all other *Phaethornis*. Male has almost straight bill and triangular central rectrices. Female has shorter and slightly decurved bill, shorter wings, more greyish underparts, and longer tail with prominent narrow central rectrices. Immature as female, with ochraceous edges to uppertail-coverts.

Habitat. Humid pre-montane and montane forests, humid secondary growth, dense shrubbery and plantations. Occurs below 2000 m, mostly below 1200 m.

Food and Feeding. Nectar and small arthropods. Flowers visited include *Heliconia*, Ericaceae, Rubiaceae and Bromeliaceae. Feeds by trap-lining.



Breeding. Season undescribed, but data on gonadal activity point to Nov-Jul. Cone-shaped nest, fastened to the underside of long, hanging leaves. 2 eggs. No further information.

Movements. Reports of seasonal movements to higher altitudes in Ecuador, but primarily sedentary. Recent record from SW Panama in Jul possibly refers to an as yet unknown breeding population.

Status and Conservation. Not globally threatened. CITES II. Generally common in wet forests; long-term survival clearly depends on habitat conservation. Commonest *Phaethornis* hermit in Pacific lowlands of Colombia, where

it replaces *P. guy* of higher elevations. Occurs in the 2000-ha Río Nambi Reserve, Nariño (S Colombia). In Ecuador, regularly recorded at El Placer, Tinalandia and Piñas.

Bibliography. Best *et al.* (1997), Borrero (1986), Butler (1979), Engelman (1997), Fjeldså & Krabbe (1990), Hilty (1975, 1997), Hilty & Brown (1986), Hinkelmann & Schuchmann (1997), Oberholser (1902), Remsen, Stiles & Scott (1986), Robbins & Ridgely (1990), Ruschi (1961d, 1981-1982), Rutgers & Norris (1972), Salaman & Mazariegos (1998b), Seutin (1998), Stotz *et al.* (1996), Vuilleumier (1978), Williams & Tobias (1994).

11. Green Hermit

Phaethornis guy

French: Ermite vert **German:** Grüner Schattenkolibri **Spanish:** Ermitaño Verde
Other common names: Guy's/White-tailed Hermit

Taxonomy. *Trochilus Guy* Lesson, 1832, Trinidad.

Race *emiliae* has often been merged into *apicalis*. Species name frequently emended to "guyi", but this is unjustified. Four subspecies currently recognized.

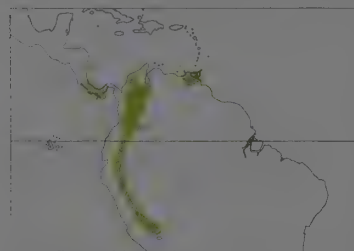
Subspecies and Distribution.

P. g. coruscus Bangs, 1902 - Costa Rica to NW Colombia.

P. g. emiliae (Bourcier & Mulsant, 1846) - Colombia (major river valleys).

P. g. apicalis (Tschudi, 1844) - E Andean slopes from N Colombia and NW Venezuela to SE Peru.

P. g. guy (Lesson, 1832) - Trinidad and NE Venezuela.



Descriptive notes. c. 13 cm; male 4-7 g, female 4-6.5 g. A medium-sized hermit hummingbird very similar to *P. yaruqui*, but with bill distinctly more curved and an always orange gular stripe. Male has nib-shaped central rectrices. Female has shorter and more decurved bill, shorter wings, lighter underparts, ochraceous belly coloration, and a longer tail due to prominent though narrow central rectrices. Immature like female but has ochraceous uppertail-coverts. Nominate is largest race, with greener upperparts and less intensely coloured underparts; races *apicalis* and *emiliae* smaller, with more intensely coloured upperparts and underparts; *apicalis* has a distinctly shorter bill than *emiliae*; W Andean *coruscus* is the brightest, most brilliant race with most extensive distribution of iridescent feathers on underparts.

Habitat. Understorey of mainly humid forest and adjacent forest edges, small clearings, secondary growth, shrubbery and plantations with dense vegetation. Recorded between 600 and 2200 m in Central America and Andean South America, but from sea-level to 1000 m in Trinidad.

Food and Feeding. Nectar of *Heliconia*, *Costus*, *Razisea*, *Columnnea*, *Pachystachys*, *Centropogon* and similar species, even of introduced plants like *Musa* and *Canna*; small arthropods. In N Andes, casual feeding in *Polylepis* woods. Feeds by trap-lining.

Breeding. Nov-Jul, in particular Jan-Apr in Trinidad; Feb-Sept, Dec in Costa Rica and Panama; data on gonadal activity indicate Jun-Aug in Colombia, and Jul-Nov in Peru. Nest construction and site similar to *P. yaruqui*; often situated near rivers and streams. Males reported to defend nest. 2 eggs; incubation 17-18 days, by female with head towards the leaf; fledging period 21-23, rarely to 27 days. Chick has dark skin and sparse down on the back, tightly closed eyes and a rudimentary bill; well feathered when about 2 weeks old.

Movements. Records away from regular range reported from Panama and N Andes, but seasonality of these probably post-breeding movements remains unclear.

Status and Conservation. Not globally threatened. CITES II. Uncommon to fairly common in most areas. In Panama, common in Darién foothills and in highlands above 600 m. Occurs in many protected areas throughout range, e.g. Monteverde Reserve and Tapantí National Park (Costa Rica), Podocarpus National Park (Ecuador), Manu National Park (Peru), Paria Peninsula National Park (Venezuela), and Asa Wright Nature Centre (Trinidad).

Bibliography. Blake, E.R. (1956), Blake, J.G. (1989), Bloch *et al.* (1991), Chapman (1926), Davis (1986), Feinsinger, Tiebout, Young & Murray (1991), Iffrench (1991), Fjeldså & Krabbe (1990), Goussard (1984), Harger (1980), Hayes & Samad (1998), Hilty & Brown (1986), Hinkelmann & Schuchmann (1997), Junge & Mees (1961), Linhart *et al.* (1987), Meyer de Schauensee & Phelps (1978), Parker *et al.* (1982), Rahbek *et al.* (1993), Remsen, Stiles & Scott (1986), Ridgely & Gwynne (1989), Robbins *et al.* (1985), Salaman & Mazariegos (1998a), Schlichmann (1995a), Skutch (1964a), Slud (1964), Snow, B.K. (1973b, 1974, 1977a, 1977b), Snow, B.K. & Snow (1972), Snow, D.W. & Snow (1964, 1980), Stiles (1979, 1980, 1981, 1985b), Stiles & Skutch (1989), Stotz *et al.* (1996), Weske & Terborgh (1977), Wetmore (1968a), Williams & Tobias (1994), Worth (1942), Zimmer (1930, 1950a).

12. White-bearded Hermit

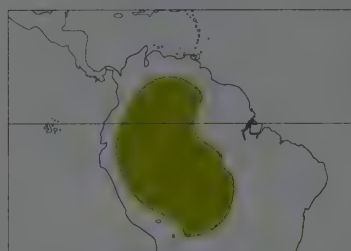
Phaethornis hispidus

French: Ermite d'Osery **German:** Weißbart-Schattenkolibri **Spanish:** Ermitaño Barbiblanco
Other common names: D'Osery's Hermit

Taxonomy. *Trochilus hispidus* Gould, 1846, Bolivia.

Wide distribution and limited knowledge of the species' notable individual variation resulted in the description of two synonyms from E. Ecuador, *oseryi* and *villosus*. Monotypic.

Distribution. Lowlands E. of Andes in Venezuela, Colombia, Ecuador, Peru, Bolivia and W Brazil.



Descriptive notes. c. 13 cm; 4-6 g. A medium-sized hermit hummingbird with bronze upperparts and grey underparts, grey margins to uppertail-coverts, and distinct gular and malar stripes of white coloration; both of these stripes show remarkable variation. Female has slightly shorter and more decurved bill and shorter wings than male. Immature differs by ochraceous margins to uppertail-coverts.

Habitat. Within the humid lowland forest region occurs mainly in regularly inundated habitats: by rivers, in *várzea* and transitional forests, less regularly in secondary growth, *Heliconia* and bamboo thickets, swamp forest

and plantations. Outside humid lowland forest region found in more humid areas such as gallery forests of *campo cerrado*, llanos and semi-deciduous forests. Occurs primarily in lowlands; in Peruvian Andes recorded up to 1200 m.

Food and Feeding. Nectar and small arthropods. Feeds by trap-lining.

Breeding. Season only locally known; breeding record Jun in Colombia; indications of active gonads Jun, Aug, Dec-Apr in Colombia; Dec in Ecuador, Jun to Dec in Peru, and Jul-Sept in Bolivia. Cone-shaped nest, fastened on underside of long, pendent leaf. 2 eggs; fledging period 20-22 days. Further aspects of breeding biology undescribed.

Movements. No information available.

Status and Conservation. Not globally threatened. CITES II. Wide distribution and adaptability probably mean that species is not threatened. Occurs in several protected areas throughout range, e.g. Manu National Park and Tambopata Reserve (Peru).

Bibliography. Bates *et al.* (1989), Best *et al.* (1997), Bond & Meyer de Schauensee (1943), Cotton (1998a), Dyrce (1990), Grantsau (1988), Gyldenstolpe (1945b), Hilty & Brown (1986), Hinkelmann & Schuchmann (1997), Meyer de Schauensee & Phelps (1978), Pearson *et al.* (1977), Remsen & Parker (1983), Remsen, Stiles & Scott (1986), Robinson (1997), Rosenberg, G.H. (1990), Ruschi (1973d, 1981-1982, 1986), Sick (1993), Stotz *et al.* (1996), Terborgh *et al.* (1984), Zimmer (1950a).

13. Western Long-tailed Hermit

Phaethornis longirostris

French: Ermite à longue queue **Spanish:** Ermitaño Colilargo Norteño
German: Westlicher Langschwanz-Schattenkolibri

Other common names: Long-billed Hermit; Jalisco Hermit (*griseoventer*); Mexican/Hartert's Hermit (*mexicanus*); Long-tailed Hermit (*longirostris*)

Taxonomy. *Ornismya longirostris* DeLattre, 1843, Guatemala.

Often considered conspecific with *P. superciliosus*, but with disjunct distributions the two are probably better treated as forming a superspecies. Some forms currently listed as races are well differentiated, and future studies may result in specific separation of *griseoventer*, *mexicanus* and *baroni*; indeed, *mexicanus* (incorporating *griseoventer*) has been recognized by some. Proposed races *veraecrucis* of S Mexico and *cassinii* from Panama and NW Colombia are inseparable from *longirostris* and *cephalus* respectively. Six subspecies currently recognized.

Subspecies and Distribution.

P. l. griseoventer Phillips, 1962 - W Mexico (Nayarit to Colima).

P. l. mexicanus Hartert, 1897 - SW Mexico (W Guerrero to SE Oaxaca).

P. l. longirostris (DeLattre, 1843) - S Mexico (N Oaxaca) to N Honduras.

P. l. cephalus (Bourcier & Mulsant, 1848) - E Honduras to NW Colombia.

P. l. sussurus Bangs, 1901 - N Colombia (Santa Marta Mts).

P. l. baroni Hartert, 1897 - W Ecuador and NW Peru.



Descriptive notes. 13-16 cm; male 5-7.5 g, female 4-6.5 g. A medium-sized hermit hummingbird with greenish-brown back and brownish or greyish underparts. Distinguishable from *P. superciliosus* and other similar species by three (instead of two) light ochraceous bands, with 2 dark bands between them, on the longest feathers of uppertail-coverts; long, decurved bill and long white tips to central rectrices. Female has shorter wings, shorter bill and an even stronger bill decurvature. Race *griseoventer* has white margins to rectrices and pale ochraceous undertail-coverts; *mexicanus* larger and darker below than

nominate; *cephalus* intergrades with *longirostris* from Guatemala to Costa Rica, with more ochraceous underparts, undertail-coverts and tail feather margins from NW to SE; N Colombian *sussurus* larger than *cephalus*, but of same coloration, whereas *baroni* has distinct greyish underparts, white margins to rectrices and whitish undertail-coverts.

Habitat. Rainforest understorey, tall secondary growth, more humid areas in semi-deciduous, pine-oak and cloudforests (in particular in S Mexico and S Ecuador), forest edge, gallery forest and plantations. Recorded from sea-level to 1000 m in Costa Rica, to 2500 m in SW Mexico and N Colombia.

Food and Feeding. Nectar and small arthropods. Resource plants include several species of *Heliconia*, *Costus*, *Aphelandra* and *Passiflora*. Feeds by trap-lining.

Breeding. May-Jul, perhaps earlier and also later in E and SE Mexico; Apr-May in S Mexico, Jan-Sept, perhaps Nov in Costa Rica; May-Sept in Panama; Jan-Apr in N Colombia; data on gonadal condition indicate May in Santa Marta Mts of N Colombia, and Jul in W Ecuador. Nest is thick-walled, cone-shaped cup of plant fibres and cobweb, fastened on the underside of a long, hanging leaf. 2 eggs; incubation 17 to 18 days, by female facing leaf; fledging 22 to 23 days. Nestling has dark skin, sparse down, tightly closed eyes, and short bill.

Movements. No information on any large-scale movements. Presumably wanders short distances.

Status and Conservation. Not globally threatened. CITES II. Small ranges of races *griseoventer*, *mexicanus* and *sussurus* indicate they are potentially at risk; significance increased by possible species status of first two. Race *cephalus* appears to be well protected in extensive network of national parks in Costa Rica, e.g. Manuel Antonio, Corcovado and Cahuita.

Bibliography. Austin (1929), Bangs & Barbour (1922), Berg (1994), Binfod (1989), Blake (1989), Blake & Loiseille (1991), Brodkorb (1943), Dearborn (1907), Des Granges (1979), Des Granges & Grant (1980), Fraga (1989), Friedmann *et al.* (1950), Gill (1987), Gill *et al.* (1982), Griseom (1932b), Hafler (1975), Hernández-Baños *et al.* (1995), Hilty & Brown (1986), Hinkelmann (1996b), Hinkelmann & Schuchmann (1997), Howell, S.N.G. &

Webb (1995a), Howell, T.R. (1957), Hudson (1984), Johnsgard (1997), Lowery & Dalquest (1951), Monroe (1968), Navarro (1992), Paynter (1957), Phillips (1962), Pople *et al.* (1997), Prestel (1983), Ridgely & Gwynne (1989), Ridgway (1911), Robbins *et al.* (1985), Rowley (1966), Russell (1964), Schaldach (1963), Skutch (1964a, 1997), Slud (1964), Stiles (1975, 1979, 1980, 1992, 1995a, 1995b), Stiles & Skutch (1989), Stiles & Wolf (1979), Tashian (1952), Todd (1942), Todd & Carriker (1922), Wetmore (1968a), Wiedenfeld *et al.* (1985), Williams & Tobias (1994), Young (1971), Zimmer (1950a).

14. Eastern Long-tailed Hermit

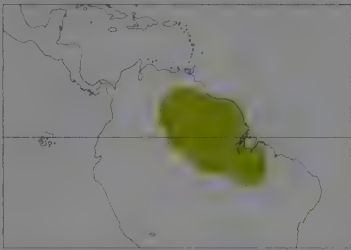
Phaethornis superciliosus

French: Ermite à brins blancs **Spanish:** Ermitaño Colilargo Común
German: Östlicher Langschwanz-Schattenkolibri
Other common names: Cayenne/Guiana/Allied/Buff-browed Hermit; Rusty-breasted Hermit (*superciliosus*)

Taxonomy. *Trochilus superciliosus* Linnaeus, 1766, Cayenne. Often considered conspecific with *P. longirostris*, but with disjunct distributions the two are probably better treated as forming a superspecies; all races of *P. malaris* except nominate have also traditionally been attributed to present species instead, but their affinities appear to lie with that species. Race *muelleri* has been associated with *P. malaris ochraceiventris*. Venezuelan birds sometimes separated as race *saturator*, but they fall within variation found in nominate race. A single hybrid of nominate *superciliosus* with *P. m. malaris* was found at a locality of sympatric occurrence. Two subspecies recognized.

Subspecies and Distribution.
P. s. superciliosus (Linnaeus, 1766) - S Venezuela, the Guianas and N Brazil (N of Amazon in Pará and Roraima).
P. s. muelleri Hellmayr, 1911 - N Brazil (S of Amazon in Pará and Maranhão).

Descriptive notes. c. 14 cm; 4-6 g. A medium-sized brownish hermit hummingbird very similar to *P. longirostris* and *P. malaris*, but distinguished from the former by two light ochraceous bands on the longest feathers of the uppertail-coverts, and from the latter, even in adult males, by a distinct gular stripe. Female has shorter wings, and a shorter, less decurved bill. Immature with light



ochraceous feather margins on the upperparts. Race *muelleri* has darker throat and breast, and in both sexes less decurved bill than nominate.

Habitat. Understorey of lowland rainforest and adjacent semi-deciduous forest, forest edge, gallery forest, second growth, riverine habitats such as river edge, *igapó* and *várzea* forest. Recorded from sea-level to 1400 m in S Venezuelan mountains.

Food and Feeding. Nectar of plants such as *Heliconia* and *Passiflora*, and small arthropods. Feeds by trap-lining.

Breeding. Breeding records in Jan, Jun, Sept and Nov in N Brazil, S of Amazon; Sept in N

Brazil, N of Amazon; Mar, Jun-Aug in Guyana; Aug-Oct in French Guiana; gonadal data indicate Nov in Brazil N of Amazon, as well as Jul and Aug in N Brazil S of Amazon. Nest similar to that of *P. longirostris*. 2 eggs; incubation at least 16 days, by female with head facing leaf, bill pointing upwards and backwards, and tail cocked up; fledging c. 21-22 days; chick has dark pinkish skin and light brown down.

Movements. No information available.

Status and Conservation. Not globally threatened. CITES II. Common throughout its range. Abundant in the Voltzberg Nature Reserve in Surinam, with recorded density of at least 3-4 pairs/km². Species is still found in bird exports from Surinam and French Guiana to EU countries, although numbers of birds exported have no detectable impact on populations.

Bibliography. Berlioz (1964), Bertin & Wilzbach (1979), Bierregaard & Lovejoy (1989), Borges (1985), Capparella (1987), Cotton (1998a), Davis (1934, 1958), Diek *et al.* (1984), Friedmann (1948), Grantsau (1988), Griscom & Greenway (1941), Haverschmidt & Mees (1994), Hinkelmann (1996a, 1996b), Hinkelmann & Schuchmann (1997), Lovejoy (1974), Meyer de Schauensee & Phelps (1978), Nicholson (1931), Novaes (1969, 1970, 1980), Oniki & Willis (1982, 1983), Prestel (1983), Ruschi (1981-1982, 1986), Rutgers & Norris (1972), Sick (1993, 1997), Skutch (1964a), Snethlage (1913, 1935), Snow (1973b), Stötz *et al.* (1996), Stauffer & Bierregaard (1995, 1996), Teixeira, Nacinovic & Luigi (1989), Teixeira, Nacinovic & Pontual (1987), Todd (1942), Tostain *et al.* (1992), Willard *et al.* (1991), Willis (1977), Young (1971), Zimmer (1950a).



15. Great-billed Hermit

Phaethornis malaris

French: Ermite à long bec **German:** Dunkler Schattenkolibri **Spanish:** Ermitaño Picogrande
Other common names: Margaretta's Hermit (*margarettae*)

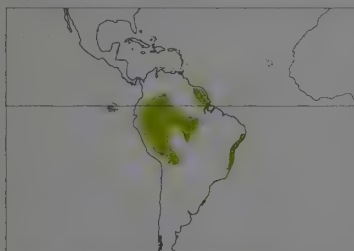
Taxonomy. *Trochilus malaris* Nordmann, 1835, Cayenne.

Often considered monotypic, but most races hitherto regarded as belonging to *P. superciliosus* apparently have closer affinities with present species. Race *ochraceiventris* may prove to merit treatment as a separate species, but this would probably not include all S Amazonian taxa of this species-group (including *P. superciliosus muelleri*), as has been suggested. Race *margarettae* has been considered a full species. Races *moorei* and *bolivianus* intergrade in E Andes of Peru, and offspring of these described as "ucayaliti". Birds occurring between lower reaches of R Madeira and R Tapajós were separated as *insignis*, but indistinguishable from *bolivianus*. Proposed race *camargoi* inseparable from *margarettae*. Six subspecies currently recognized.

Subspecies and Distribution.

P. m. insolitus Zimmer, 1950 - E Colombia, S Venezuela, adjacent N Brazil.
P. m. malaris (Nordmann, 1835) - Surinam and French Guiana to CN Brazil (Amapá).
P. m. margarettae Ruschi, 1972 - coastal E Brazil (Pernambuco to Espírito Santo).
P. m. moorei Lawrence, 1858 - E Colombia, E Ecuador and N Peru.
P. m. ochraceiventris Hellmayr, 1907 - NE Peru and W Brazil to lower R Madeira (S of Amazon).
P. m. bolivianus Gould, 1861 - SE Peru, Bolivia and W Brazil to W bank of R Tapajós (S of Amazon).

Descriptive notes. 13-17 cm; male 4.5-10 g, female 4-8 g. Medium-sized to large hermit similar to *P. superciliosus*, but with gular stripe faint or absent in adult male; like *P. longirostris*, but with only two pale ochraceous bands on longest uppertail-coverts. Female has shorter wings and bill, latter slightly more decurved. Immature has pale ochraceous feather margins on upperparts. Nominant race is largest, with darkest underparts; *insolitus* very similar to *malaris* but smaller, intergrades with *moorei*, which has paler, greyer underparts. Race *bolivianus* smaller than *moorei*, with dark brown throat and breast and orange-ochraceous belly; very similar, perhaps with



paler underparts and different tail coloration, is geographically distant *margarettae*. Race *ochraceiventris* larger than last three, with breast and belly bright orange.

Habitat. Understorey of unindented lowland rainforest of the *terra firme*, pre-montane and humid upper tropical forest, transitional forest, second growth, bamboo thickets, shrubbery; race *ochraceiventris* found in *igapó* forest. Usually below 600 m, but up to 1500 m in Colombian and 1650 m in Bolivian Andes, though recorded up to 2400 m.

Food and Feeding. Nectar of *Heliconia*, *Pitcairnia*, etc. and small arthropods. Feeds by trap-lining.

Breeding. Occupied nests Aug-Dec, French Guiana; gonadal activity Jun-Sept in Bolivia, Jun-Nov in Peru. Nest as in *P. longirostris*. 2 eggs; incubation 14-15+ days, by female; fledging probably 20-23 days.

Movements. No information available.

Status and Conservation. Not globally threatened. CITES II. Race *margarettae*, limited to forest remnants in E Brazil, could be threatened by further habitat destruction.

Bibliography. Blake (1962), Capparella (1987), Dick *et al.* (1984), Fjeldså & Krabbe (1989), Goussard (1984), Grantsau (1988), Haverschmidt & Mees (1994), Hinkelmann (1988b, 1989b, 1996a, 1996b), Hinkelmann & Schuchmann (1997), King (1978/79), McKay (1980), Mees (1977b), Novaes (1974, 1976), Parker *et al.* (1982), Peres & Whittaker (1991), Phelps & Phelps (1958), Pinto (1978), Prestel (1983), Remsen, Stiles & Scott (1986), Robbins *et al.* (1991), Ruschi (1972, 1973d, 1976a, 1981-1982, 1982a, 1986), Schulenberg *et al.* (1984), Seilern (1934), Sick (1993, 1997), Snow (1981), Stotz *et al.* (1996), Teixeira, Naciniovic & Luigi (1989), Teixeira, Naciniovic & Pontual (1987), Terborgh & Weske (1975), Terborgh *et al.* (1984), Todd (1942), Tostain *et al.* (1992), Zimmer (1950a).

16. Tawny-bellied Hermit

Phaethornis syrmatorphorus

French: Ermite à ventre fauve **Spanish:** Ermitaño Ventrihabano
German: Orangebauch-Schattenkolibri
Other common names: Trainbearing/Baron Rothschild Hermit

Taxonomy. *Phaethornis syrmatorphorus* Gould, 1851, western Ecuador.

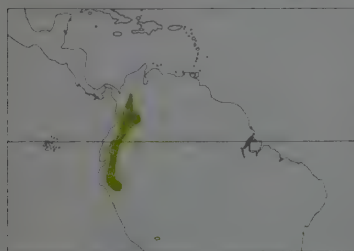
Closest to *P. koepckeae* and *P. philippii*. Races well distinguished and might be different species. Description of *berlepschi* based on an immature bird of nominate race; *huallagae*, described for birds from N Peru, is inseparable from *columbianus*. Two subspecies currently recognized.

Subspecies and Distribution.

P. s. syrmatorphorus Gould, 1851 - W Andes of Colombia (including Cauca/Patía Valley) to SW Ecuador.
P. s. columbianus Boucard, 1891 - E Andes of Colombia, including S Magdalena Valley, to N Peru.

Descriptive notes. c. 14 cm; 5-7 g. A medium-sized hermit hummingbird with a prominent long, distinctly decurved bill, olive-green upperparts and reddish-orange uppertail-coverts; belly, undertail-coverts and tail feather margins bright orange. Female has slightly more decurved bill and shorter wings. Immature has light ochraceous margins to feathers of upperparts, giving a scaly appearance. Race *columbianus* differs in having a dark brown (instead of orange) throat and breast, and often has some white feathers on breast and belly.

Habitat. Understorey of humid montane forest, sometimes at forest edge or in dense second growth. Generally between 1000 and 2300 m, although records exist between 750 and 3100 m.



Food and Feeding. Nectar and small arthropods. Feeds by trap-lining.

Breeding. Recorded Jun in Ecuador; gonadal activity Dec in Peru; birds in breeding condition Mar-Aug and Dec in Colombia. Elongated, cone-shaped nest made of dry leaves, vegetable fibres, and fern scales, surrounded by silk and attached to underside tip of pendulous leaf. 2 eggs. No further data.

Movements. No information available. Presumably resident.

Status and Conservation. Not globally threatened. CITES II. Habitat loss may be a severe threat in the future. Regularly recorded in Cueva de los Guácharos National Park, and La Planada and Rio Nambi Reserves, Colombia; also at Mindo, Coca Falls, between Baeza and Tena, and near Piñas, Ecuador.

Bibliography. Best & Clarke (1991), Best, Clarke *et al.* (1993), Best, Heijnen & Williams (1997), Bloch *et al.* (1991), Butler (1979), Davies *et al.* (1994), Fjeldså & Krabbe (1990), González (1998), Graves (1985), Hilty (1997), Hilty & Brown (1986), Hinkelmann & Schuchmann (1997), Marin & Carrión (1994), Miller (1963), Parker *et al.* (1982), Rahbek *et al.* (1993), Remsen, Stiles & Scott (1986), Ridgely & Gaulin (1980), Robbins & Ridgely (1990), Salaman & Mazariagos (1998b), Stotz *et al.* (1996), Zimmer (1950a).

17. Koepcke's Hermit

Phaethornis koepckeae

French: Ermite de Koepcke **Spanish:** Ermitaño de Koepcke
German: Orangebrauner Schattenkolibri

Taxonomy. *Phaethornis koepckeae* Weske and Terborgh, 1977, Cerros del Sira, Peru.

In past, sometimes placed in genus *Ametornis*. Closely related to *P. philippii*, replacing it at higher elevations; also related to *P. syrmatorphorus*. Significant differences in size between some populations may be the result of long-term isolation. Monotypic.

Distribution. Slopes of isolated mountains along E Andes in Peru.



Descriptive notes. c. 13 cm; male 4-6 g, female 4-5.5 g. Medium-sized hermit with straight bill, olive-green upperparts, orange-red uppertail-coverts, and bright orange underparts. Similar to *P. syrmatorphorus columbianus*, but without white feathers on breast and belly. In contrast to *P. philippii*, has dark brown throat with whitish malar and gular stripes. Female has shorter bill and wings; very slight decurvature in female bill visible. Immature has ochraceous feather margins on the upperparts.

Habitat. Moist upper tropical forest understorey, rarely in second growth. Recorded between 270 and 1130 m.

Food and Feeding. Nectar and small arthropods. Feeds by trap-lining.

Breeding. Gonadal activity Aug-Oct. Small conical nest similar to that of other *Phaethornis*, attached to the underside of a long pendulous leaf near its tip. 2 eggs; nest with 2 young found Jul.

Movements. No information available. Presumably resident.

Status and Conservation. Not globally threatened. CITES II. Currently considered Near-threatened. Has been found so far at no more than 10 localities. Regularly recorded at Amazonia Lodge, near Manu National Park (Peru), at an old tea plantation situated between subtropical and tropical forests, at altitude of 457 m.

Bibliography. Davis (1986), Hinkelmann (1987, 1988b), Hinkelmann & Schuchmann (1997), Meyer de Schauensee (1982), Parker *et al.* (1982), Remsen, Stiles & Scott (1986), Stotz *et al.* (1996), Vuilleumier & Mayr (1987), Weske & Terborgh (1977).

18. Needle-billed Hermit

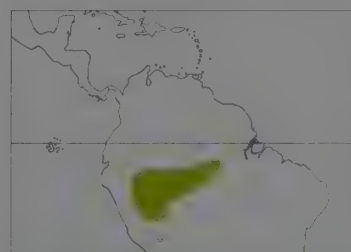
Phaethornis philippii

French: Ermite de Filippi **Spanish:** Ermitaño Picoaguja
German: Orangefarbener Schattenkolibri

Taxonomy. *Trochilus Philippii* Bourcier, 1847, Bolivia.

In past, sometimes placed in genus *Ametornis*. Closely related to *P. koepckeae*, replacing it at lower elevations; also related to *P. syrmatorphorus*. Monotypic.

Distribution. E Peru, N Bolivia and W Brazil (S of Amazon to W bank of R Tapajós).



Descriptive notes. c. 12 cm; male 4-6 g, female 4-5.5 g. A straight-billed hermit hummingbird, smaller than *P. koepckeae*, but very similar in coloration, with entire throat, breast and belly orange. Female has shorter wings and bill, but with almost no visible curvature. Immature has ochraceous feather margins on upperparts.

Habitat. Understorey of lowland rainforest, sometimes at forest edge; occurs in *terra firme*, *várzea*, bamboo thickets and plantations. Recorded up to 325 m.

Food and Feeding. Nectar and small arthropods. Feeds by trap-lining.

Breeding. Gonadal activity Jun and Jul in Peru and N Bolivia. No further information available.

Movements. No information available.

Status and Conservation. Not globally threatened. CITES II. Locally common in understorey of lowland forest especially in E Peru (e.g. Tambopata Reserve). Status of population in W Brazil is not known.

Bibliography. Allen (1995), Donahue (1994), Dyrce (1990), Forrester (1993), Grantsau (1988), Hilty & Brown (1986), Hinkelmann (1988b), Hinkelmann & Schuchmann (1997), Novaes (1957, 1976), Parker & Remsen (1987), Parker *et al.* (1982), Peres & Whittaker (1991), Remsen & Traylor (1989), Remsen, Stiles & Scott (1986), Robbins *et al.* (1991), Ruschi (1981-1982, 1986), Sick (1993), Stotz, Fitzpatrick *et al.* (1996), Stotz, Lanyon *et al.* (1997), Traylor (1958a), Zimmer (1950a).

On following pages: 19. Straight-billed Hermit (*Phaethornis bourcierii*); 20. Pale-bellied Hermit (*Phaethornis anthophilus*); 21. Scale-throated Hermit (*Phaethornis eurynome*); 22. Planalto Hermit (*Phaethornis pretrei*); 23. Sooty-capped Hermit (*Phaethornis augusti*); 24. Buff-bellied Hermit (*Phaethornis subochraceus*); 25. Dusky-throated Hermit (*Phaethornis squalidus*); 26. Streak-throated Hermit (*Phaethornis rupurumii*); 27. Little Hermit (*Phaethornis longuemareus*); 28. Minute Hermit (*Phaethornis idaliae*); 29. Cinnamon-throated Hermit (*Phaethornis nattereri*); 30. Reddish Hermit (*Phaethornis ruber*); 31. White-browed Hermit (*Phaethornis stuarti*); 32. Black-throated Hermit (*Phaethornis atrimentalis*); 33. Stripe-throated Hermit (*Phaethornis striigularis*); 34. Grey-chinned Hermit (*Phaethornis griseogularis*).

19. Straight-billed Hermit

Phaethornis bourcieri

French: Ermite de Bourcier

German: Braunbauch-Schattenkolibri

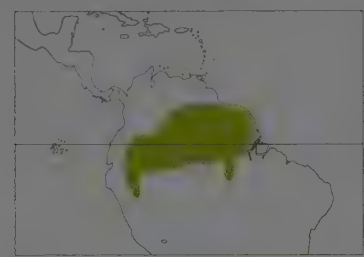
Spanish: Ermitaño Piquirrecto

Taxonomy. *Trochilus Bourcieri* Lesson, 1832, Cayenne.

In past, sometimes placed in genus *Ametromis*. Morphological characters argue against close relationship to other hermits with straight bills, *P. philippii* and *P. koepckeae*. Many authors have accepted additional race *whitelyi* for northern birds, but claimed characters correspond to individual variation, both types of coloration occurring throughout range of nominate race. Two subspecies recognized.

Subspecies and Distribution.

P. b. bourcieri (Lesson, 1832) - E Colombia and N Peru to S Venezuela, Guianas and Brazil N of Amazon.
P. b. major Hinkelmann, 1989 - Brazil S of Amazon along E bank of lower R Tapajós.



Descriptive notes. 12-13 cm; 4-5 g. Medium-sized hermit with olive-green upperparts and brownish ("whitelyi coloration") to greyish ("bourcieri coloration") underparts; straight bill. Female has shorter wings and bill; almost no curvature visible in bill. Immature has light ochraceous edging to feathers of upperparts. Race *major* significantly larger in all measurements, with plumage coloration similar to nominate form with greyish underparts.

Habitat. Understorey of lowland *terra firme* rainforest, and dense areas of adjacent semi-deciduous or pre-montane forest, up to 1600 m in S Venezuelan mountains; occasionally at forest edge, in bamboo thickets, dense shrubbery, *várzea* forest, second growth or plantations.

Food and Feeding. Nectar and small arthropods. Recorded at flowers of *Manettia*, *Guzmania* and *Vriesea*; feeds by trap-lining.

Breeding. Mar-May in Brazil; active nests Sept in Manaus and Amapá, Brazil, Oct in French Guiana, Sept in Colombia; gonadal activity Sept in Colombia, and Jul, Aug, Oct, Nov in Peru. Nest is long, cone-shaped cup of plant matter and cobweb fastened under tip of long, hanging leaf. 2 eggs; incubation 17-18 days, by female; fledging c. 23 days. At hatching, chick has eyes closed and down scattered over body.

Movements. No information available.

Status and Conservation. Not globally threatened. CITES II. Common throughout its range. Regularly seen in primary forest at the Voltzberg Nature Reserve, Surinam, with local population density of at least 2-3 pairs/km². Occurs in several protected areas, e.g. Amacayacu National Park (Colombia) and Imataca Forest Reserve (Venezuela).

Bibliography. Bierregaard & Lovejoy (1989), Cotton (1998a), Dickerman & Phelps (1982), Friedmann (1948), Grantsau (1988), Haverschmidt & Mees (1994), Hilty & Brown (1986), Hinkelmann (1989a), Hinkelmann & Schuchmann (1997), Meyer de Schauensee & Phelps (1978), Oniki & Willis (1982), Parker *et al.* (1982), Remsen, Stiles & Scott (1986), Rosenberg, G.H. (1990), Ruschi (1981-1982, 1986), Snow (1981), Stotz *et al.* (1996), Stouffer & Bierregaard (1995, 1996), Tostain *et al.* (1992), Weske & Terborgh (1977), Willard *et al.* (1991), Willis (1977), Zimmer (1950a).

20. Pale-bellied Hermit

Phaethornis anthophilus

French: Ermite anthophile

German: Fleckenkehl-Schattenkolibri

Spanish: Ermitaño Ventripálido

Other common names: Black-cheeked Hermit

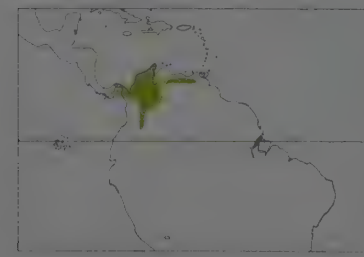
Taxonomy. *Trochilus anthophilus* Bourcier, 1843, upper Magdalena Valley, Colombia.

In past, sometimes placed in genus *Ametromis*. An almost straight-billed hermit without close relatives, somewhat resembling *P. euryome*. A melanistic bird of doubtful origin was described as race *fuliginosus*, but never verified as referring to a valid population. Birds of nominate race in E Andes of Colombia have smaller wings and bill than other populations and may be separable as *fuscescapillus*, which these differences also be confirmed in Venezuelan birds. Two subspecies recognized.

Subspecies and Distribution.

P. a. hyalinus Bangs, 1901 - Pearl Is (off Pacific coast of Panama).

P. a. anthophilus (Bourcier, 1843) - C Panama to Colombia (Magdalena Valley and E of Andes) and N Venezuela.



Descriptive notes. c. 13 cm; male 4.5-5.5 g, female 4-5 g. A medium-sized hermit hummingbird with dark green to olive-green upperparts and light grey underparts, distinguishable from all other *Phaethornis* of similar size by lack of a gular stripe, which is replaced by light feather fringes giving a scaly or striped appearance. Male has almost straight bill. Female has shorter wings and bill clearly decurved. Immature has light ochraceous feather margins on the upperparts. Racial differences slight; *hyalinus* has lighter coloration of underparts and more bluish green than dark green upperparts.

Habitat. Semi-deciduous forest and several types of drier woodland, second growth, brushy edges, thorny thickets, plantations and gallery forest. Recorded from sea-level to about 1500 m.

Food and Feeding. Nectar of *Heliconia*, *Brownea*, etc., and small arthropods. Feeds by trap-lining.

Breeding. Nest construction recorded Dec in Colombia; breeding Oct-Feb and Apr in Venezuela; gonadal condition indicates Apr and Jun in Venezuela, and Oct-Mar in Colombia. Cone-shaped cup nest attached under tip of a pendent leaf as typical for the genus. 2 eggs. No further details.

Movements. Records Apr and Dec in NE Venezuela may indicate regular movements; more data needed.

Status and Conservation. Not globally threatened. CITES II. Uncommon to locally common. Abundant in drier areas of coastal Venezuela and at head of Magdalena Valley, Colombia. Population near Santa Marta shows density of at least 1-2 pairs/km². Occurs in Tayrona and Henri Pittier National Parks, in NE Colombia and NC Venezuela respectively.

Bibliography. Durlington (1931), Friedmann & Smith (1950, 1955), Hilty & Brown (1986), Hinkelmann & Schuchmann (1997), Mack & Fisher (1990), Meyer de Schauensee & Phelps (1978), Miller (1952), Ridgely & Gwynne (1989), Schäfer & Phelps (1954), Schuchmann (1984a), Stiles (1995c), Stotz *et al.* (1996), Todd & Carriger (1922), Wetmore (1939, 1946, 1968a).

21. Scale-throated Hermit

Phaethornis euryome

French: Ermite euryome

German: Schuppenkehl-Schattenkolibri

Spanish: Ermitaño Escamoso

Other common names: Black-billed Hermit ("nigrirostris")

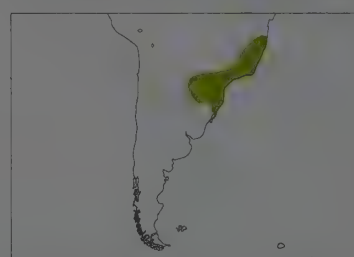
Taxonomy. *Trochilus euryome* Lesson, 1832, Brazil.

Similar to *P. anthophilus*, both species apparently lacking close relatives. Includes "*P. nigrirostris*", based on a unique specimen of nominate race with uniformly black bill. Two subspecies recognized.

Subspecies and Distribution.

P. e. paraguayensis M. Bertoni & W. Bertoni, 1901 - E Paraguay and NE Argentina (Misiones).

P. e. euryome (Lesson, 1832) - SE Brazil (Bahia to Rio Grande do Sul).



Descriptive notes. c. 14 cm; male 4.5-6 g, female 4-5 g. Medium-sized hermit, olive above and greyish below, having dark throat feathers with narrow light-coloured edges, giving a scaly appearance; with broad white tail feather margins and yellowish lower mandible. Female has shorter wings and slightly more decurved bill. Race *paraguayensis* is identical in coloration but significantly smaller.

Habitat. Understorey of lowland and montane rainforest, humid areas in semi-deciduous forest, especially in SW of range, and old second growth. In N of range, common in mountainous regions. Recorded at 100-2250 m.

Food and Feeding. Nectar taken from *Heliconia*, *Centropogon*, *Costus*, *Neoregelia*, *Nidularium*, *Reichsteineria*, *Sinningia*, *Siphocampylus*, *Impatiens*, *Besleria*, *Passiflora*, *Quesnelia*, *Tillandsia*, *Vriesea*, *Aechmea*, *Canistrum*, *Alstroemeria*, *Salvia*, *Dahlstedtia*, *Nematanthus*, *Jacobinia*, *Manettia* and other plant species, and small arthropods. Feeds by trap-lining.

Breeding. Sept-Mar in Brazil. Long cone-shaped cup of plant material and cobweb attached to inner tip of leaf of a palm, fern, *Heliconia*, etc. Nests are often decorated with *Spiloma*, a lichen releasing red pigment when in contact with the breeding female. As a consequence, both the bird's underparts and eggs take on a pink coloration. 2 eggs; incubation about 17 days, by female; fledging 22-23 days.

Movements. No information available. Presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Common throughout its range. In forest patches in the Tibagi Basin, Paraná, Brazil, population density recorded as at least 1-2 pairs/km². Frequently recorded in Iguazú Falls National Park, in both Brazil and Argentina. Occurs in Serra dos Orgãos and Itatiaia National Parks.

Bibliography. Belton (1984), Brooks *et al.* (1993), Canevari *et al.* (1991), Fischer (1994), Gonzaga *et al.* (1995), Grantsau (1988), Hayes (1995), Hinkelmann (1988b), Hinkelmann & Schuchmann (1997), Höfling & Lencioni (1992), King (1978/79), Lowen, Bartrina, Clay & Tobias (1996), Lowen, Clay *et al.* (1995), Mayr & Vuilleumier (1983), Oniki (1996), de la Peña (1994), do Rosário (1996), Ruschi (1973a, 1981-1982, 1982a, 1986), Saibene *et al.* (1996), Sazima *et al.* (1995), Scott & Brooke (1985), Sick (1979, 1993, 1997), Snow & Snow (1986), Snow & Teixeira (1982), Storer (1989), Stotz *et al.* (1996), Willis (1992), Willis & Oniki (1981).

22. Planalto Hermit

Phaethornis pretrei

French: Ermite de Prêtre

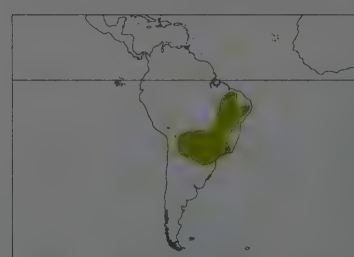
German: Zimtroter Schattenkolibri

Spanish: Ermitaño del Planalto

Taxonomy. *Trochilus Pretrei* Lesson and DeLattre, 1839, Minas Gerais, Brazil.

Forms superspecies with *P. augusti*. Proposed races "*garleppi*" and "*pallidiventris*" based on aberrant specimens; *schwarti* (Bahia) and *minor* (N Goiás, S Maranhão) based on individual variation. Monotypic.

Distribution. Bolivia, N Argentina and Paraguay to Brazil S of Amazonian rainforest area.



Descriptive notes. c. 14 cm; male 4.5-5.5 g, female 4-5 g. Medium-sized hermit with olive-green upperparts, prominent reddish upperpart-coverts, cinnamon-red underparts, and a distinctly elongated second (next to central) pair of rectrices with prominent white tips. Female has shorter wings and shorter, less decurved bill. Immature has pale feather fringes on upperparts.

Habitat. Non-forest, vegetation-rich areas, or dry forest, predominantly in mountainous regions, also second growth, forest edge and gallery forest. Also well adapted to human environments if rich in trees and herbs. Found between 400 and 2100 m.

Food and Feeding. Nectar of various flowering plants; small arthropods. Probably feeds by trap-lining.

Breeding. Sept-Apr in Brazil; nest records in Sept in NW Argentina and Aug in Brazil. Nest is a long, cone-shaped cup constructed of plant matter and spider web, but, in contrast to other *Phaethornis*, fixed on vertical structure like roots and twigs, or protected in cavity on rock face or similar situation; other sites include on wires in man-made hollows like culverts, waste-water pipes, under bridges and even in abandoned buildings. Sometimes a suitable site will be used again, and a new nest is constructed on the old one. 2 eggs; incubation about 15 days, by female; fledging at least 20 days. Chick has a roseate skin coloration. Male observed in the nest vicinity in the breeding period.

Movements. No reliable information available; thought to be partly migratory within certain areas.

Status and Conservation. Not globally threatened. CITES II. Common throughout range. Accepts man-made habitats, e.g. gardens, parks. In SE Brazil, abundance varies from 2 pairs/km² in natural habitats to at least 5 pairs/km² in larger city parks. Occurs in several protected areas, e.g. Callegua National Park (Argentina) and Serra dos Orgãos, Serra da Canastra and Serra do Cipó National Parks (Brazil).

Bibliography. Bond & Meyer de Schauensee (1943), Camperi (1990), Canevari *et al.* (1991), Castellano & Moreyra (1986), Cintra & Yamashita (1990), Contreras (1986), Contreras *et al.* (1990), Esteban (1947), Fjeldså & Krabbe (1990), Fjeldså & Mayer (1996), Forrester (1993), Fraga *et al.* (1984), Grantsau (1988), Hayes (1995), Hinkelmann & Schuchmann (1997), Marini *et al.* (1997), Mitchell (1957), Nores & Yzurieta (1981), Oniki (1996), Pacheco (1997), de la Peña (1994), Remsen & Traylor (1989), Remsen, Stiles & Scott (1986), do Rosário (1996), Ruschi (1950c, 1951, 1975a, 1973d, 1976d, 1981-1982, 1982a, 1986), Saibene *et al.* (1996), Schmitt *et al.* (1997), Short (1975), Sick (1993, 1997), Sick & Teixeira (1981), da Silva & Oniki (1988), Stager (1961), Storer (1989), Stotz *et al.* (1996), Tobias *et al.* (1993), Todd (1942), Willis (1979).

23. Sooty-capped Hermit

Phaethornis augusti

French: Ermite d'Auguste **German:** Graubauch-Schattenkolibri **Spanish:** Ermitaño Limpicaca

Taxonomy. *Trochilus augusti* Bourcier, 1847, Caracas, Venezuela.

Forms superspecies with *P. pretrei*. Includes "*P. fumosus*", based on melanistic specimen of nominate. Colombian birds described as race *vicarius* do not differ from nominate. Three subspecies recognized.

Subspecies and Distribution.

P. a. curiosus Wetmore, 1956 - Santa Marta Mts (N Colombia).

P. a. augusti (Bourcier, 1847) - E Andes and Macarena Mts (Colombia), and coastal Cordillera (Venezuela).

P. a. incanescens (Simon, 1921) - isolated mountains of S Venezuela and W Guyana.



Descriptive notes. c. 14-15 cm; male 4-5-6 g, female 4-5 g. Medium-sized hermit, very similar to *P. pretrei*, but with uniform grey underparts. Differs from *P. hispidus* by rufous uppertail-coverts and prominent white tips to elongated second rectrices (next to central pair). Female has shorter wings and more decurved bill, but these differences less evident than in similar species. Immature has pale feather margins on upperparts. Racial differences slight: *curiosus* has palest underparts and broadest, though indistinct, white gular stripe of all populations; *incanescens* differs by having narrower and less intensely coloured uppertail-coverts.

Habitat. Understorey of semi-deciduous and fairly dry to humid montane forest, dense vegetation in mainly mountainous non-forest habitats, forest edge, second growth and plantations. Recorded to 1800 m in S Venezuelan highlands and to 3500 m in N Venezuelan Andes; rarely below 500 m.

Food and Feeding. Nectar, taken by by trap-lining; small arthropods, sometimes sought in buildings.

Breeding. Active nests found Feb-Jul and Sept-Dec in N Venezuela. Nest-site and construction similar to *P. pretrei*, and with a peculiar counterweight constructed of pieces of dried mud attached to the nest wall by spider web to create stability. Clutch size 2. Breeding biology is probably very like that of *P. pretrei*, but there is no additional information.

Movements. Probably mostly sedentary, but some seasonal vertical movement and straggling noted.

Status and Conservation. Not globally threatened. CITES II. Common to locally uncommon. Easy to see in coastal Cordillera of Venezuela and in Santa Marta Mts of Colombia, with density of at least 1-2 pairs/km². Appears to adapt well to habitats modified by man, so probably quite secure. Occurs in Guatopo, Cueva del Guácharo and Henri Pittier National Parks (Venezuela).

Bibliography. Chubb (1916), Fjeldså & Krabbe (1990), Forrester (1993), Friedmann & Smith (1955), Gilliard (1941, 1959), Grantsau (1988), Hilty & Brown (1986), Hinkelmann & Schuchmann (1997), Mayr & Phelps (1967, 1971), Meyer de Schauensee & Phelps (1978), Ruschi (1981-1982, 1986), Schäfer & Phelps (1954), Sick (1993), Snyder (1966), Stotz *et al.* (1996), Thomas (1993), Wetmore (1939).

24. Buff-bellied Hermit

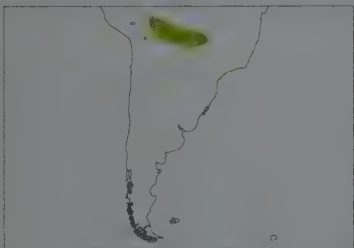
Phaethornis subochraceus

French: Ermite ocré **German:** Ockerbauch-Schattenkolibri **Spanish:** Ermitaño Ocráceo

Taxonomy. *Phaethornis subochraceus* Todd, 1915, Santa Cruz de la Sierra, Bolivia.

Like *P. squalidus* and other small hermits, but more closely related to *P. pretrei* and *P. augusti*. Monotypic.

Distribution. E Andean lowlands of Bolivia and adjacent Brazil (Mato Grosso).



Descriptive notes. 11-12 cm; 3-5-4 g. A small, dull brownish hermit hummingbird with ochraceous (buff) belly, best told by distinctly elongated second pair of rectrices and prominent white margins on all rectrices. Female has shorter wings than male. Immature has pale feather margins on upperparts.

Habitat. Undergrowth in hilly, deciduous and dry semi-deciduous forest, second growth, open woodland and shrubs. Recorded at 150-800 m.

Food and Feeding. Nectar and small arthropods. No additional information available.

Breeding. Birds in breeding condition in Jun, Jul and Oct, Bolivia. No reliable description of nest.

Incubation said to be by female and to last 14-15 days, fledging 20 days; but data require confirmation.

Movements. No information available. Presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Locally common. Poorly known, and should perhaps be classed as Data-deficient. Regularly recorded in dry deciduous forest near Samaipata (EC Bolivia) and in Pantanal of Mato Grosso (WC Brazil). Very rare in scientific collections.

Bibliography. Bond & Meyer de Schauensee (1943), Cintra & Yamashita (1990), Davis (1993), Dubs (1992), Forrester (1993), Grantsau (1988), Hinkelmann & Schuchmann (1997), Meyer de Schauensee (1982), Remsen & Traylor (1989), Remsen, Schmitt & Schmitt (1990), Remsen, Stiles & Scott (1986), Ruschi (1981-1982, 1986), Sick (1993, 1997), Short (1975), Stotz *et al.* (1996), Willis & Oniki (1990).

25. Dusky-throated Hermit

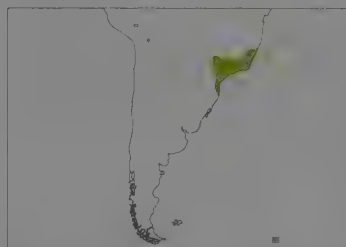
Phaethornis squalidus

French: Ermite terne **German:** Dunkelkehl-Schattenkolibri **Spanish:** Ermitaño Escualido
Other common names: Sooty-throated Hermit

Taxonomy. *Trochilus squalidus* Temminck, 1822, Ipanema, São Paulo, Brazil.

One of the small hermits sometimes separated in genus *Pygornis*; present species has the most primitive characters of any member of this group, linking these species with the larger members of genus *Phaethornis*. Often considered to include *P. rupurumii*, but morphological characters indicate that that species is more closely related to *P. longuemareus* and *P. idaliae*. Proposed race "*maranhaoensis*", sometimes considered a full species, has proved to be the hitherto undescribed adult male plumage of *P. nattereri*. Monotypic.

Distribution. SE Brazil (S Minas Gerais and Espírito Santo to Santa Catarina).



Descriptive notes. 10-11 cm; 2-5-3-5 g. A small, dull brownish hermit, intermediate in size, though sometimes as small as some individuals of the small species; brownish ochraceous underparts and a dark brown throat. Sexes alike in coloration, measurements and bill curvature.

Habitat. Understorey of humid littoral and adjacent montane forest, and dense secondary growth. Recorded from sea-level to 2250 m.

Food and Feeding. Nectar and small arthropods. No detailed studies.

Breeding. Oct-Feb. Nest is cone-shaped cup attached to the inner tip of a long, pendent leaf. 2 eggs; incubation given as 14 days, by female.

and fledging said to be 20-22 days; data require confirmation.

Movements. No information available. Presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Recorded as frequent in Tijuca National Park near Rio de Janeiro. Continuing destruction of rainforest may present a major threat in future.

Bibliography. Aleixo & Galetti (1997), dos Anjos *et al.* (1997), Forrester (1993), Grantsau (1988), Hinkelmann & Schuchmann (1997), Meyer de Schauensee (1982), Oniki (1996), Parker & Goerck (1997), Pinto (1954), do Rosário (1996), Ruschi (1981-1982, 1982a, 1986), Scott & Brooke (1985), Sick (1993), Stotz *et al.* (1996), Tobias *et al.* (1993), Willis (1992).

26. Streak-throated Hermit

Phaethornis rupurumii

French: Ermite balafré **German:** Strichelkehl-Schattenkolibri **Spanish:** Ermitaño del Rupununi

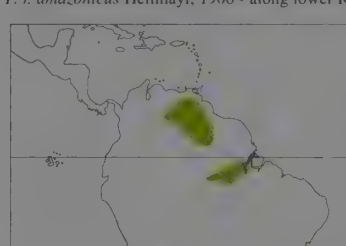
Taxonomy. *Phaethornis* [sic] *Rupurumii* Boucard, 1892, Rupununi River, Guyana.

One of the small hermits sometimes separated in genus *Pygornis*. Often considered conspecific with *P. squalidus*, but morphological characters indicate it is more closely related to *P. longuemareus* and *P. idaliae*. Future studies may reveal that geographically isolated race *amazonicus* should be considered a full species. A hybrid of present species with *P. longuemareus* was described as "*P. longuemareus imatacae*"; another with *P. ruber ruber* as "*P. longuemareus aethopyga*". Two subspecies recognized.

Subspecies and Distribution.

P. r. rupurumii Boucard, 1892 - extreme E Colombia (E Vichada) through C & E Venezuela and W Guyana to adjacent N Brazil.

P. r. amazonicus Hellmayr, 1906 - along lower R Amazon in NC Brazil.



Descriptive notes. 10-11 cm; 2-5-3 g. Like *P. squalidus* in size and coloration, but differs in having white (nominate) or sometimes light buffy (*amazonicus*) instead of ochraceous undertail-coverts, and a brownish grey (nominate) instead of ochraceous belly. Adult male has more intensely dark brown throat feathers, presenting a streaky appearance. Female has broader light margins to rectrices than male. Immature resembles adult female.

Habitat. Understorey of rainforest edge, várzea forest and various drier habitats drier, e.g. semi-deciduous forest, gallery forest and forest islands in non-forest regions, thickets, second

growth, scrub, etc.; along both banks of lower Amazon in "*campos* islands" with corresponding vegetation adapted to drier conditions. Mainly lowlands, but up to 500 m in Venezuela and Guyana.

Food and Feeding. Nectar and small arthropods, but no detailed information.

Breeding. No information available.

Movements. No information available.

Status and Conservation. Not globally threatened. CITES II. At least locally common. Very poorly known, and should perhaps be classed as Data-deficient. Frequently recorded (*rupurumii*) near Puerto Ayacucho, Venezuela, and (*amazonicus*) near Manaus, Brazil.

Bibliography. Cherrie (1916), Chubb (1916), Forrester (1993), Grantsau (1988), Hilty & Brown (1986), Hinkelmann (1996a), Hinkelmann & Schuchmann (1997), Meyer de Schauensee & Phelps (1978), Moskovits *et al.* (1985), Pinto (1947), Ruschi (1981-1982, 1986), Sergeant (1994a), Sick (1993, 1997), Sneath (1913), Snyder (1966), Stotz *et al.* (1996), Zimmer & Hilty (1997).

27. Little Hermit

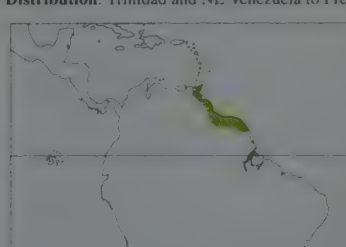
Phaethornis longuemareus

French: Ermite nain **German:** Brauner Zwergschattenkolibri **Spanish:** Ermitaño Chico
Other common names: Longuemare's/Rusty-breasted Hermit

Taxonomy. *Trochilus Longuemareus* Lesson, 1832, Cayenne.

One of the small hermits sometimes separated in genus *Pygornis*. Usually considered to include *P. idaliae*, *P. atrimentalis* and *P. strigularis*; morphological characters, however, indicate that they should be treated as separate species, with latter two not even very closely related to present species; *P. idaliae* is closest relative. Invalid races proposed include: "*imatacae*" based on hybrid of present species with *P. rupurumii*; and "*aethopyga*" based on hybrid of *P. rupurumii* with *P. ruber ruber*. Monotypic.

Distribution. Trinidad and NE Venezuela to French Guiana.



Descriptive notes. 9 cm; male 3-3-8 g, female 2-5-3-8 g. A small hermit hummingbird with olive-green upperparts, orange-ochraceous belly, white undertail-coverts, and clearly pointed central rectrices. Smaller than *P. squalidus* and *P. rupurumii*. Male has intensely dark brown throat. Female has less extensive dark throat coloration and broader buff margins to rectrices than male. Immature resembles adult female.

Habitat. Typically occurs in understorey of various more open forest habitats like swamp and mangrove forest, dense second growth, thickets, scrub, forest edge, or plantations on

South American mainland. In Trinidad, however, preferred habitat is rainforest. Recorded from sea-level to 700 m.

Food and Feeding. Nectar of *Heliconia*, *Pachystachys*, *Costus*, *Palicourea*, *Mandevilla*, *Justicia*, *Cephaelis* and many other flowering plants, and small arthropods. Feeds by trap-lining.

Breeding. Dec-Jun, but most nests Jan-Mar in Trinidad. Active nests were found in Jan and Aug in Surinam; Jan, Jul and Aug in French Guiana. Nest is a long cone-shaped cup of plant material and cobweb, attached to the underside tip of a pendent leaf. 2 eggs. No further data.

Movements. No information available. Presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Common to locally common. In the Arima Valley of Trinidad, population densities of at least 3-5 pairs/km²; at the Voltzberg Nature Reserve in Surinam, at least 1 pair/km². Occurs in Asa Wright Nature Centre (Trinidad).

Bibliography. Arp (1957), Bangs & Penard (1918), Chubb (1916), Dobkin (1987), Feinsinger (1983), Iffrench (1991), Haverschmidt & Mees (1994), Hayes & Samad (1998), Herklots (1961), Hinkelmann (1988c, 1990a, 1990b, 1996a), Hinkelmann & Schuchmann (1997), Junge & Mees (1961), Meyer de Schauensee & Phelps (1978), Phelps & Phelps (1952, 1958), Ruschi (1981-1982, 1986), Rutgers & Norris (1972), Snow, B.K. & Snow (1972), Snow, D.W. (1968), Snow, D.W. & Snow (1964), Snyder (1966), Stotz *et al.* (1996), Tostain *et al.* (1992), Wiley (1971).

28. Minute Hermit

Phaethornis idaliae

French: Ermite d'Italie **German:** Schiller-Zwergschattenkolibri **Spanish:** Ermitaño Pigmeo

Taxonomy. *Trichilus idaliae* Bourcier and Mulsant, 1856, Rio de Janeiro, Brazil.

One of the small hermits sometimes separated in genus *Pygmornis*. Often considered a race of *P. longuemareus*, its closest relative, but sexual dimorphism and other morphological characters indicate that they should be treated as separate species. Monotypic.

Distribution. SE Brazil (Bahia to Rio de Janeiro).



Descriptive notes. 8 cm; 2-2.5 g. Very small, sexually dimorphic hermit with pointed central rectrices and dark green iridescent upperparts. Male has dark brown throat, with some patchy iridescent feathers on breast. Female has orange-ochraceous throat and breast, and broader tail feather margins than male; underparts remarkably similar in coloration to female *P. longuemareus*, but that species larger. Immature female like adult female; immature male has breast darker than adult female, but paler than adult male; tail feather margins as broad as in female.

Habitat. Understorey of primary or only slightly disturbed littoral forest, forest edge,

old secondary growth, forest islands within the coastal *cerrado* (*restinga*). Occurs below 500 m.

Food and Feeding. Nectar and small arthropods. Feeds by trap-lining.

Breeding. Oct-Feb. Nest similar to *P. longuemareus*; 2 eggs; incubation by female, at least 14 days; fledging 20 days, sometimes more.

Movements. No information available. Presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Atlantic Forest Lowlands EBA. Confined to a vulnerable rainforest habitat, further destruction of which may pose a severe threat to the survival of the species; should perhaps be classed as Data-deficient or Near-threatened. Occurs in Rio Doce State Park (Minas Gerais) and Sooretama Biological Reserve (Espírito Santo). Rare in scientific collections.

Bibliography. Forrester (1993), Grantsau (1988), Hinkelmann & Schuchmann (1997), Oniki (1996), Parker & Goerck (1997), Ruschi (1967c, 1981-1982, 1982a, 1986), Scott & Brooke (1985), Sick (1969, 1993, 1997), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Tobias *et al.* (1993), Willis (1992).

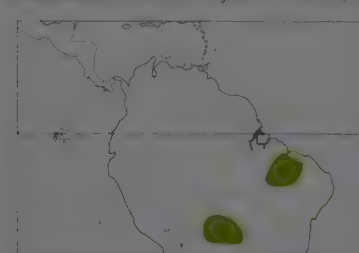
29. Cinnamon-throated Hermit

Phaethornis nattereri

French: Ermite de Natterer **German:** Zimtkehl-Schattenkolibri **Spanish:** Ermitaño de Natterer
Other common names: Maranhão Hermit

Taxonomy. *Phaethornis nattereri* Berlepsch, 1887, Caiçara and Engenho da Gama, Mato Grosso. One of the small hermits sometimes separated in genus *Pygmornis*. Similar to *P. subochraceus* and *P. squalidus*, but morphological characters indicate a closer relationship to *P. ruber*, *P. stuarti*, *P. atrimentalis*, *P. strigularis* and *P. griseogularis*. Recently described "*P. maranhensis*", which was considered a full species or a race of *P. squalidus*, has proved to be the hitherto undescribed adult male plumage of present species. The two populations appear to be geographically isolated. Monotypic.

Distribution. E Bolivia and adjacent SW Brazil (Mato Grosso); also NE Brazil (Maranhão to Ceará).



Descriptive notes. 10 cm; 2.5-3 g. Small hermit, smaller and paler brown than *P. squalidus* and *P. subochraceus*, but larger than most congeners; has ochraceous undertail-coverts. Throat coloration in adult male more intense than in female, but not as dark as in the dark-throated species *P. longuemareus*, *P. rapurumii*, *P. idaliae* and *P. atrimentalis*. Central rectrices of adult male pointed and thus similar to those species, not rounded as in the remainder. With these, *P. ruber*, *P. stuarti*, *P. atrimentalis*, *P. strigularis* and *P. griseogularis*, shares elongated reddish unbanded uppertail-coverts. Female same size as adult male, differing by lighter throat and

longer central rectrices. Immature resembles adult female.

Habitat. Inhabits variety of vegetation-rich habitats outside rainforest; semi-deciduous forest, second growth, thickets, *cerrado*, arboreal *caatinga*, forest islands and gallery forest. Occurs below 500 m.

Food and Feeding. Nectar of *Pavonia*, *Helicteres*, *Ruellia*, *Bauhinia* and other flowering plants, as well as small arthropods. Feeds by trap-lining.

Breeding. No information available.

Movements. No information available. Presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Poorly known, and should perhaps be classed as Data-deficient. Perhaps locally common. In Brazil, occurs in Chapada dos Guimarães

National Park (Mato Grosso) and in dry woodlands of Araguaia National Park (Goiás). Sometimes also reported as occurring along lower R Amazon in Pará, although validity of reports doubtful. Rare in scientific collections.

Bibliography. Bates *et al.* (1989), Dubs (1992), Forrester (1993), Grantsau (1968a, 1988), Hinkelmann (1988a, 1988b, 1990b), Hinkelmann & Schuchmann (1997), Mayr & Vuilleumier (1983), Olmos (1993), Pinto (1978), Remsen & Traylor (1989), Ruschi (1953a, 1967a, 1981-1982, 1986), Sargeant (1996), Sick (1993, 1997), da Silva & Oniki (1988), Stotz *et al.* (1996), Vuilleumier & Mayr (1987), Willis & Oniki (1990).

30. Reddish Hermit

Phaethornis ruber

French: Ermite roussâtre **German:** Roter Zwergschattenkolibri **Spanish:** Ermitaño Rojizo
Other common names: Red-vented/Pygmy Hermit

Taxonomy. *Trichilus ruber* Linnaeus, 1758, Surinam.

One of the small hermits sometimes separated in genus *Pygmornis*. Forms a species group or even superspecies with *P. stuarti*, and the two are often considered conspecific; there is very close geographical contact, if not sympatry, and one natural hybrid recorded. Other close relatives are *P. atrimentalis*, *P. strigularis* and *P. griseogularis*. There is a zone of character introgression between nominate and race *longipennis*, but no such zone has been found between present species and *P. stuarti*. Future investigation may confirm species status for current races *nigricinctus* and *episcopus*, other taxa apparently lacking introgression with nominate *ruber*. Birds of SE Brazil have been separated as race *pygmaeus*, but claimed differences took insufficient account of age- and sex-related individual variation homogeneously distributed over entire range of nominate race. Synonyms for species include *P. rufiventris* and *P. rufigaster*. A hybrid of nominate *ruber* with *P. rapurumii* was described as "*P. longuemareus aethopyga*". Four subspecies recognized.

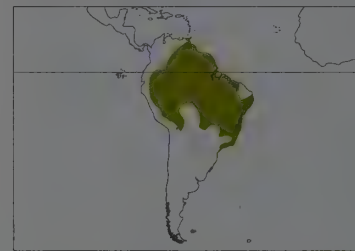
Subspecies and Distribution.

P. r. episcopus Gould, 1857 - C & E Venezuela, Guyana and adjacent N Brazil.

P. r. ruber (Linnaeus, 1758) - Surinam and French Guiana through Brazil to SE Peru and N Bolivia.

P. r. nigricinctus Lawrence, 1858 - extreme SW Venezuela and E & S Colombia to N Peru.

P. r. longipennis Berlepsch & Stolzmann, 1902 - S Peru.



Descriptive notes. 8-9 cm; 2-3 g. A small hermit hummingbird with dark green upperparts and cinnamon-rufous underparts. Male regularly has some dark feathers forming a patch or even a band on the breast, and a shorter tail with rounded rectrices showing narrow white or reddish tips. Female has paler breast and belly coloration, with longer wings and tail, the rectrices having broader margins than in male. Immature resembles adult female, male with shorter wings. Adult male of *episcopus* also has white margins to rectrices; this race is same size as nominate and coloration of underparts tends more to orange-rufous than cinnamon-rufous of *ruber*;

nigricinctus smallest, with adult male having the most intense rufous underparts and white instead of rufous tail feather margins, while female differs in size from nominate; *longipennis* is largest and closest to *P. stuarti* in having a whitish chin, while prominent tips to central rectrices are rufous and thus same colour as light margins of all tail feathers in this race as well as in nominate.

Habitat. Understorey of lowland, pre-montane and littoral rainforest of the *terra firme*, *várzea* and semi-deciduous forest, forest edge and forest islands in more open habitats, as well as *cerrado*, savanna woodland, thickets and second growth. Mainly in the lowlands, but recorded to 1500 m in S Peru, 1200 m in N Bolivia, and 1100 m in Venezuela.

Food and Feeding. Nectar and small arthropods. Flowering plants visited include *Trichanthera*, *Petreaea*, *Costus*, *Dahlstedtia*, *Nematanthus*, *Psychotria* and many others. In SE Brazil, nectar robbery by piercing the corolla base appears to be a regular feeding strategy. Feeds by trap-lining.

Breeding. May-Oct in NE Brazil, Oct-Feb in SE Brazil; active nests found in Jan, May-Oct in the Guianas. Data on gonadal condition indicate Nov in S Peru; Jun, Aug in N Peru. Nest is cone-shaped cup of diverse plant fibres, leaves, mosses, lichens, seed plumes and cobweb fastened to the inner tip of a long, hanging leaf. 2 eggs; incubation 15-17 days, by female, sitting with her bill directed towards the leaf; fledging period between 15 and 22 days. Chick has roseate skin with two lines of light brown down on the back; eyes open at 6 days old. Female cares for her offspring for a few days after they leave the nest. In the Belém area, cells of *Pison* wasps appear to be a regular occurrence in the lower part of the nest, though there is no obvious advantage for the bird.

Movements. No reliable information available. Presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Locally common to abundant. Sites at which species is frequently recorded include: Imataca Forest Reserve, Bolívar (Venezuela); several localities around Georgetown (Guyana); near Mana and in Nouragues (French Guiana); Serra dos Órgãos National Park, Rio de Janeiro, and around Porto Seguro and Boa Nova, Bahia (Brazil); and near Satja, between Santa Cruz and Cochabamba (Bolivia). In Voltzberg Nature Reserve, Surinam, recorded density of at least 2-4 pairs/km².

Bibliography. Bates *et al.* (1989), Bond & Meyer de Schauensee (1943), Davis, T.A.W. (1934, 1958), Davis, T.J. (1986), Dubs (1992), Dyrce (1990), Forrester (1993), Friedmann (1948), Goussard (1984), Grantsau (1988), Gyldestolpe (1945b), Haverschmidt (1954b), Haverschmidt & Mees (1994), Hilty & Brown (1986), Hinkelmann (1986, 1996a), Hinkelmann & Schuchmann (1997), Meyer de Schauensee & Phelps (1978), Novaes (1970, 1973, 1980), Oniki (1970), Oniki & Willis (1983), Peres & Whittaker (1991), Pinto (1953), Remsen, Stiles & Scott (1986), Robens & Robens (1984), Ruschi (1949a, 1973d, 1981-1982, 1982a, 1986), Rutgers & Norris (1972), Sazima *et al.* (1995), Schuchmann (1986), Sick (1993, 1997), Sick & Teixeira (1981), Sneath (1982a, 1982b, 1935), Snow (1973b), Stager (1961), Stotz *et al.* (1996), Terborgh & Weske (1969), Terborgh *et al.* (1984), Tostain *et al.* (1992), Willard *et al.* (1991), Willis (1977), Zimmer (1950a).

31. White-browed Hermit

Phaethornis stuarti

French: Ermite de Stuart **German:** Stuarts Zwergschattenkolibri **Spanish:** Ermitaño Boliviano

Taxonomy. *Phaethornis stuarti* Hartert, 1897, Salinas, River Beni, Bolivia.

One of the small hermits sometimes separated in genus *Pygmornis*. Forms a species group or even superspecies with *P. ruber*, of which often considered a race; there is very close geographical contact, if not sympatry, and one natural hybrid recorded but no zone of character introgression. Other close relatives are *P. atrimentalis*, *P. strigularis* and *P. griseogularis*. Monotypic.

Distribution. SE Peru to C Bolivia.



Descriptive notes. c. 9 cm; male 2-2.5 g, female 2-3 g. A small hermit hummingbird very similar to *P. ruber*, in particular to race *longipennis*, from which it is distinguishable by white tail feather margins and prominent white tips to central rectrices. Sexual dimorphism as in *P. ruber*.

Habitat. Understorey of transitional forest (between *várzea* and *terra firme* rainforest), bamboo thickets, second growth, hilly tropical forest, scrub and similar habitats. Recorded to 1000 m.

Food and Feeding. Nectar and small arthropods. No detailed information available.

Breeding. No information available.

Movements. No information available. Presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Very poorly known, and should probably be classed as Data-deficient; research and survey work required. Regularly seen between Cuzco and Manu, SE Peru.

Bibliography. Bond & Meyer de Schauensee (1943), Brace *et al.* (1997), Hinkelmann (1996a), Hinkelmann & Schuchmann (1997), Meyer de Schauensee (1982), Olrog (1968), Parker *et al.* (1982), Remsen & Parker (1983), Remsen & Taylor (1989), Stotz *et al.* (1996), Terborgh *et al.* (1984), Zimmer (1950a).

32. Black-throated Hermit

Phaethornis atrimentalis

French: Ermite à gorge noire

German: Schwarzkehl-Schattenkolibri

Spanish: Ermitaño Barbinegro

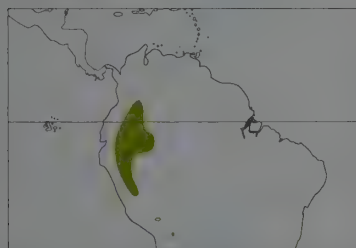
Taxonomy. *Phaethornis atrimentalis* Lawrence, 1858. Napo, Ecuador.

One of the small hermits sometimes separated in genus *Pygornis*. Frequently considered conspecific with *P. longuemareus*, but morphological characters indicate closest relationship is to *P. ruber* and *P. stuarti*. Other close relatives are *P. striigularis* and *P. griseogularis*. Two subspecies recognized.

Subspecies and Distribution.

P. a. atrimentalis Lawrence, 1858 - E Andes of Colombia, Ecuador and N Peru.

P. a. riojae (Berlepsch, 1889) - C Peru.



Descriptive notes. 8-9 cm. Very similar to *P. ruber*, but easily distinguishable by prominent dark brown throat and whitish undertail-coverts. Male has a more intensely coloured throat, shorter wings than female (not regularly in race *riojae*), and, as adult, narrower tail feather margins. The central rectrices are usually rounded, but pointed ones also occur. Dark feathers on the cinnamon-red breast, forming a dark patch or even a band, are regularly found in males. Race *riojae* is significantly larger than nominate.

Habitat. Understorey of lowland rainforest, in particular at edges, second growth areas, zones transitional to more open habitats, plantations, swamp forest. Usually in lowlands but recorded in Andes S of Marañón Valley to 1200 m.

Food and Feeding. Nectar of flowering plants like *Costus*, *Aechmea*, *Palicourea*, *Drymonia*, *Gurania*, *Pitcairnia*, as well as small arthropods.

Breeding. No nest yet described. Data on gonadal activity indicate breeding in Jul and Nov (Peru), and Sept (Ecuador).

Movements. No information available. Presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Present in Río Nambi Reserve, Nariño, and Amacayacu National Park, S Amazonas (Colombia); also recorded near Tingo María (C Peru).

Bibliography. Hilty & Brown (1986), Hinkelmann (1988c, 1990a, 1990b), Hinkelmann & Schuchmann (1997), McKay (1980), Remsen, Stiles & Scott (1986), Schulenberg *et al.* (1984), Snow (1981), Zimmer (1930, 1950a).

33. Stripe-throated Hermit

Phaethornis striigularis

French: Ermite à gorge rayée

German: Streifenkehl-Schattenkolibri

Spanish: Ermitaño Gorgiestriado

Other common names: Dusky/Boucard's Hermit (*saturatus* = *adolphi*)

Taxonomy. *Phaethornis striigularis* Gould, 1854. Bogotá, Colombia.

One of the small hermits sometimes separated in genus *Pygornis*. Often considered conspecific with *P. longuemareus*, but morphological characters indicate closest relationship is to *P. griseogularis*; race *saturatus* in particular is extremely similar to *P. g. griseogularis*. Other close relatives include *P. atrimentalis*, *P. ruber* and *P. stuarti*. Race *saturatus* (= *adolphi*) sometimes treated as a separate species. Further races proposed in Mexico (*cordobae* = *adolphi*) and Panama (*nelsoni* = *fraterculus*) judged invalid, as claimed differences fail to take into account age- and sex-related variation in *saturatus*. In NW Colombia, races *saturatus*, *subrufescens* and *striigularis* come together in a zone of character introgression. Name *adolphi* pre-dates *saturatus*, but considered to be preoccupied by almost identical name; *adolphi* therefore subsequently replaced by *cordobae*, but this in turn becomes junior synonym of *saturatus*. Four subspecies currently recognized.

Subspecies and Distribution.

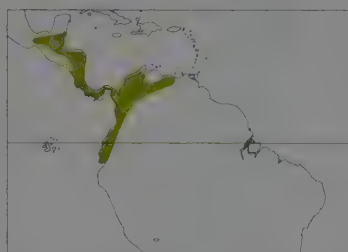
P. s. saturatus Ridgway, 1910 - S Mexico (S Veracruz) to NW Colombia.

P. s. subrufescens Chapman, 1917 - W Colombia and W Ecuador.

P. s. striigularis Gould, 1854 - N Colombia (and Magdalena Valley) and adjacent W Venezuela.

P. s. ignobilis Todd, 1913 - N Venezuela.

Descriptive notes. c. 9 cm; male 2-3 g, female 2-3.2 g. A small hermit hummingbird, olive-green above, brownish to greyish below, with darker throat than breast and belly, but without dark breast feathers. Adult male has clearly rounded central rectrices with lighter narrow margins. Female has longer wings, less intensely coloured throat and breast, more pointed central rectrices with broader margins than male. Immature resembles adult female. Races well differentiated: nominate *striigularis* has throat feathers with light margins, creating a streaky appearance; this character also evident in



subrufescens and *ignobilis*, though less distinct; nominate has palest and greyest underparts; *subrufescens* and *ignobilis* have brown-ochraceous throat and breast, more intense and less grey in *subrufescens*; race *saturatus* is brightest, with ochraceous orange underparts and rufous instead of ochraceous tail feather margins.

Habitat. Understorey of humid tropical lowland and hilly forest, in tree-gaps, clearings and forest edge, dense second growth woodland, vegetation-rich plantations and even gardens; races *striigularis* and *ignobilis* additionally in semi-deciduous forest, scrub and thickets. Recorded from sea-level to 1300 m in Venezuela, 1500 m in Costa Rica and 1800 m in W Ecuador.

Food and Feeding. Nectar of a large variety of flowers with medium-sized or small corollae, and small arthropods. Nectar robbery by piercing the corolla bases of *Scutellaria* and *Pavonia* observed in Costa Rica and Panama respectively. Feeds by trap-lining.

Breeding. May-Jul in S Mexico; Apr-Jul, Nov, Dec, with records Sept and Feb (or possibly even all year round) in Costa Rica; active nests recorded Jul in W Colombia, Jan-Mar in W Ecuador, May and Jun in Belize. Data on gonadal condition indicate breeding Mar and May in N Colombia; Mar and Dec in W Colombia, May in Panama, and Apr in Honduras. Nest is compact, cone-shaped cup of plant material including fibres and down, held together by cobweb, attached to the underside tip of a long, hanging leaf. 2 eggs; incubation 15-16 days, by female; fledging period 20-23 days. Chick has pink skin, with a double row of light brownish down on the back; eyes remain closed until 10 days old.

Movements. No information. Seasonal occurrence in N Venezuela may indicate some migration.

Status and Conservation. Not globally threatened. CITES II. Common throughout its range, especially along the Pacific coast of Colombia. In the Anchiwayá Valley, near Buenaventura, SW Colombia, population density at least 1-2 pairs/km². Occurs in Manuel Antonio, Braulio Carrillo and Corcovado National Parks (Costa Rica).

Bibliography. Arp (1957), Berg (1994), Binford (1989), Blake (1989), Blake & Loiselle (1991), Brosset (1964), Brown & Bowers (1985), Butler (1979), Feinsinger (1976, 1980), Fogden (1993), Friedmann *et al.* (1950), González-García (1993), Haffer (1975), Hilty (1975, 1997), Hilty & Brown (1986), Hinkelmann (1988c, 1990a, 1990b), Hinkelmann & Schuchmann (1997), Howell, S.N.G. & Webb (1995a), Howell, T.R. (1957), Johnson (1997), Land (1970), Meyer de Schauensee & Phelps (1978), Monroe (1968), Pople *et al.* (1997), Ridgely & Gwynne (1989), Ridgway (1911), Roubik (1982), Russell (1964), Schäfer & Phelps (1954), Schuchmann (1987a), Skutch (1951, 1964a), Slud (1964, 1980), Smith (1966), Stiles (1979, 1980, 1985b, 1992, 1995b), Stiles & Skutch (1989), Stone (1996), Todd & Carriker (1922), Van Tyne (1935), Vuilleumier (1978), Wetmore (1968a), Williams & Tobias (1994), Willis & Eisenmann (1979), Zimmer (1950a).

34. Grey-chinned Hermit

Phaethornis griseogularis

French: Ermite à gorge grise

German: Binden-Zwergschattenkolibri

Spanish: Ermitaño Barbigrís

Other common names: Grey-throated Hermit; Gould's Hermit (*zonura*); Porculla Hermit (*porcullae*)

Taxonomy. *Phaethornis griseogularis* Gould, 1851. Bogotá, Colombia.

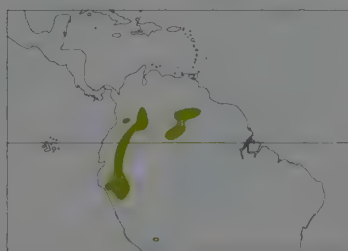
One of the small hermits sometimes separated in genus *Pygornis*. Closest to *P. striigularis*. Other close relatives include *P. atrimentalis*, *P. ruber* and *P. stuarti*. Races *zonura* and *porcullae* are rare in scientific collections, and latter may be classed as separate species when more detailed information is available; *zonura* has been treated as synonym of nominate *griseogularis*. Three subspecies currently recognized.

Subspecies and Distribution.

P. g. griseogularis Gould, 1851 - W of Andes in Colombia; E Andes from Colombia to N Peru; S & SE Venezuela and adjacent N Brazil on several isolated mountains.

P. g. zonura Gould, 1860 - NW Peru (Cajamarca and adjacent Amazonas).

P. g. porcullae Carriker, 1935 - W Andean mountains in NW Peru (Tumbes, Piura and Lambayeque).



Descriptive notes. 8-10 cm; male 2-2.5 g, female 2-3 g. Very similar to *P. striigularis*, but always distinguishable by pointed outer primaries, and prominent grey band on upperside of central rectrices between the usually blackish base and the whitish tip; presence and extent of black breast band variable. Sexual dimorphism as *P. striigularis*; male has greyish throat and rounded rectrices with narrow light margins. Female has longer wings, lighter underparts, and longer rectrices with broader margins. Immature resembles adult female. Nominat *griseogularis* significantly smaller than *P. striigularis saturatus*, but has similar coloration on under-

parts. Races *zonura* and *porcullae* larger than nominate, with *porcullae* being largest and similar in size to *P. nattereri* or *P. longuemareus*. Where *zonura* differs by paler, more greyish underparts and a more decurved bill, *porcullae* has even lighter underparts and white margins on the 3 inner pairs of rectrices; these margins are white with some ochraceous in the outermost rectrices.

Habitat. Understorey of humid pre-montane, subtropical and lower montane cloudforest, forest edge, dense second growth, thickets, in E Colombia also in gallery forest; race *zonura* prefers dry tropical woodland, and *porcullae* humid woodland and moist forest remnants in seasonally dry forest. Usually between 600 and 2000 m; in E Colombia recorded below 400 m.

Food and Feeding. Nectar and small arthropods. Feeds by trap-lining.

Breeding. Gonadal data indicate breeding in Oct in Colombia; Jan, May and Jun in NW Peru. Nest hitherto undescribed, breeding biology presumably similar to *P. striigularis*.

Movements. No information available. Presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Limited distribution of races *zonura* and *porcullae* could be a cause for future concern. Nominat race regularly recorded between Garzón and Florencia (SC Colombia), and along Loreto road between Tena and Coca (E Ecuador).

Bibliography. Barrowclough & Escalante (1990), Barrowclough *et al.* (1995), Best & Clarke (1991), Bloch *et al.* (1991), Butler (1979), Davis (1986), Grantsau (1988), Hilty & Brown (1986), Hinkelmann (1990b), Hinkelmann & Schuchmann (1997), Meyer de Schauensee & Phelps (1978), Phelps & Phelps (1965), Rahbek *et al.* (1993), Remsen, Stiles & Scott (1986), Ruschi (1981-1982, 1986), Salaman & Mazariegos (1998a, 1998b), Schuchmann (1987a), Sick (1993, 1997), Stotz *et al.* (1996), Willard *et al.* (1991), Williams & Tobias (1994), Zimmer (1950a).

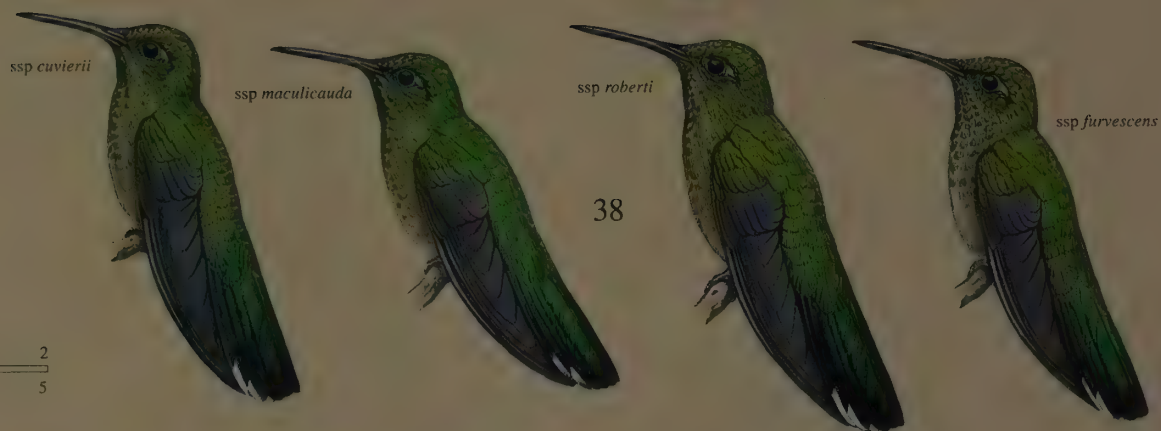
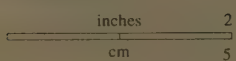


PLATE 47



Subfamily TROCHILINAE

Genus *ANDRODON* Gould, 1863

35. Tooth-billed Hummingbird

Andron aequatorialis

French: Colibri d'Équateur **German:** Zahnschnabelkolibri **Spanish:** Colibrí Piquidentado
Other common names: Ecuadorian Toothbill, Equatorial/Cadet Hummingbird

Taxonomy. *Andron aequatorialis* Gould, 1863, Ecuador. Controversial discussion continues as to whether this species belongs in Phaethornithinae or Trochilinae. Based on external morphology, hindneck musculature, and behaviour it has even been placed, together with members of genus *Doryfera*, in a separate subfamily Doryferinae, phylogenetically ranked between the hermits and non-hermits. Behavioural and molecular studies suggest that the species is not related to the Phaethornithinae. Monotypic.

Distribution. E Panama and W Colombia (Chocó) to NW Ecuador.



Descriptive notes. 13.2-14.2 cm (including 4 cm of bill); male 9 g, female 7 g. Male has straight bill with hooked tip, distal half or less with backward-pointing tooth-like serrations, black above, yellow below tipped dark; forehead sooty brown, crown metallic reddish copper, back green, rump reddish copper, tail-coverts dull greenish blue, bordered above by a narrow white band; underparts greyish, sides of head, throat and breast broadly streaked black; tail rounded, greyish green, with dark subterminal band and broad white tips. Female like male, but lacks hook on bill, duller on crown, less heavily streaked below. Immature

has crown and nape greenish blue, coppery band on rump small or lacking.

Habitat. Occurs from sea-level to 1100 m, mainly in understorey of primary forest. Forages from middle to lower strata; occasionally found at forest edge and in secondary growth along ravines.

Food and Feeding. Forages for nectar at flowering shrubs and epiphytes such as Ericaceae and Gesneriaceae. The tooth-like serrations are perfectly suited to collecting main prey, spiders, from leaves, embankment cavities, or narrow holes; occasionally male probes with hooked bill in curled dead leaves in search of arthropod prey. Feeds mainly by trap-lining.

Breeding. Reproductive biology virtually unknown. Indirect evidence for breeding season is indicated by enlarged gonads of individuals in SW Colombia Jan-Mar; in NW Ecuador males gather at leks during Feb-May in forest understorey.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Common resident of undisturbed primary forest, with densities of at least 3-5 individuals/km². Seems to have disappeared in parts of SW Colombia (N & W Buenaventura) due to extensive logging; present in Río Nambi Reserve (Pasto area).

Bibliography. Anon. (1998a), Best *et al.* (1997), Butler (1979), Gill & Gerwin (1989), Hilty (1997), Hilty & Brown (1986), Meyer de Schauensee (1982), Ridgely & Gwynne (1989), Robbins *et al.* (1985), Salaman (1996), Salaman & Mazariegos (1998b), Schuchmann (1992, 1995b), Selander (1966), Stotz *et al.* (1996), Wetmore (1968a).

Genus *DORYFERA* Gould, 1847

36. Green-fronted Lancebill

Doryfera ludovicae

French: Porte-lance de Louise **Spanish:** Colibrí Picolanza Mayor
German: Grünstirn-Lanzettschnabel

Taxonomy. *Trochilus ludovicae* Bourcier and Mulsant, 1847, Buena Vista, east Andes above Villavicencio, Meta, Colombia.

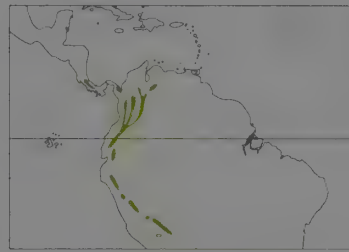
Genus formerly placed in subfamily Phaethornithinae, due largely to confusion regarding its nest; now known to be part of the basal radiation of the Trochilinae; in many older works generic name *Hemistephania* was used. Two proposed races, *rectirostris* (W Andes of Colombia and NW Ecuador) and *grisea* (NW Bolivia), now usually subsumed into nominate race; former differs only in bill averaging longer, but with wide overlap, and latter based on characters of an immature male, birds of this age being indistinguishable from those of nominate. Species name sometimes misspelt *ludoviciae*. Two subspecies currently recognized.

Subspecies and Distribution.

D. l. veraguensis Salvin, 1867 - NC Costa Rica to W Panama.

D. l. ludovicae (Bourcier & Mulsant, 1847) - extreme E Panama (Cerro Tacarcuna), Colombia and W Venezuela S through Andes to NW Bolivia (E slope only from C Ecuador southwards).

Descriptive notes. 11-13 cm; male 5.9 g and female 5.5 g in *veraguensis*, male 6.4 g and female 6.0 g in *ludovicae*. Male of nominate with frontlet glittering pale green, crown and nape dark coppery-bronze, shading to bronzy-green on back; uppertail-coverts blue, tinged grey-blue distally; tail black, narrowly tipped with dull grey; underparts dull, dark greenish bronze, darker and greener on throat. Female similar but frontlet usually smaller and sometimes lacking, underparts greyer on average, grey tips to rectrices usually broader. Race *veraguensis* smaller and more dichromatic; male darker.



dusky green below, darker bronze on crown and nape providing increased contrast with frontlet; female greyer below with more purplish bronze crown, paler grey tips to rectrices. Immature tends to be greyer below and with duller bronzy crown and reduced frontlet.

Habitat. Mid-strata and lower canopy of wet, epiphyte-laden cloudforest and humid forest in broken terrain, with male more often along ridges while female prefers ravines and gorges, particularly for nesting. Especially outside breeding season, often along forest edges and into tall second growth, sometimes down to shrub height. Mainly 750-2300 m (rarely to

2600 m) in Costa Rica and Panama, 900-2400 m in Colombia, in some areas descending to lower elevations outside breeding season.

Food and Feeding. In forest usually visits flowers of epiphytes with long, tubular, usually pendent corollas, including Ericaceae (*Satyria*, *Psammisia*, *Cavendishia*, *Macleania*), Loranaceae (*Psittacanthus*), Rubiaceae and Gesneriaceae, preferring to hover beneath flower without clinging (for which the slightly upturned bill is ideal); usually trap-lines dispersed clumps, but during breeding season male may defend rich clumps. Outside forest may visit flowers with short or long corollas, including many Rubiaceae, Gesneriaceae, etc. Frequently flycatches, sallying from perch in canopy or along stream, or hover-hawks, especially low over streams; also hover-gleans arthropods from vegetation.

Breeding. In Costa Rica breeds in latter half of wet season to start of dry, Aug-Jan; in Colombia nesting recorded between Jul and late Jan. Nest a rather bulky cup of moss, treefern scales, fine fibres and cobwebs in dark, usually humid site; generally attached to hanging rootlet or vine under rock overhang in dark ravine or gorge (in which case lower part often elongated to form a cylindrical structure) but sometimes attached to wire under bridge or roof; less often on small ledge in gorge or cave. Clutch 2; incubation (one nest) 19 days; fledging period 25+ days (young frightened by people, might have left 1-2 days later if undisturbed).

Movements. Outside breeding season in Costa Rica many individuals descend to 500 m, rarely down to 150 m on Caribbean slope; no information available on other populations.

Status and Conservation. Not globally threatened. CITES II. Generally uncommon to locally fairly common in suitable habitat throughout range, which includes several protected areas for both races, e.g. Tapanti National Park (Costa Rica), Río Nambi Reserve (Colombia) and Paschoa Forest Reserve (Ecuador). Will tolerate moderate disturbance caused by selective logging and forest fragmentation, and evidently can take advantage of remnant forest strips along streams as corridors for altitudinal movements.

Bibliography. Bond & Meyer de Schauensee (1943), Fjeldså & Krabbe (1990), Hilty (1997), Hilty & Brown (1986), Meyer de Schauensee & Phelps (1978), Remsen, Traylor & Parkes (1986), Ridgely & Gwynne (1989), Ridgway (1911), Ruschi (1961d), Salaman & Mazariegos (1998b), Slud (1964), Snow, B.K. & Gochfeld (1977), Snow, D.W. & Snow (1980), Stattersfield *et al.* (1998), Stiles (1985b), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968a), Williams & Tobias (1994), Zimmer (1950a).

37. Blue-fronted Lancebill

Doryfera johannae

French: Porte-lance de Jeanne **Spanish:** Colibrí Picolanza Menor
German: Blaustirn-Lanzettschnabel

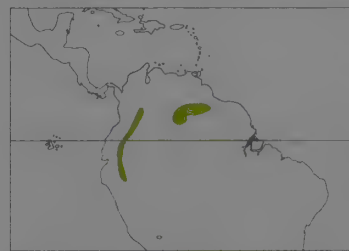
Taxonomy. *Trochilus Johanna* Bourcier, 1847, Peru.

Genus formerly placed in subfamily Phaethornithinae, due largely to confusion regarding its nest; now known to be part of the basal radiation of the Trochilinae; in many older works generic name *Hemistephania* was used. Two subspecies recognized.

Subspecies and Distribution.

D. j. johannae (Bourcier, 1847) - E slope of E Andes from CE Colombia to NE Peru.

D. j. guianensis (Boucard, 1893) - S Guyana, S Venezuela and tepuis of adjacent N Brazil.



Descriptive notes. 10-11 cm; male 4.2 g, female 3.9 g. Long, very slender, slightly upturned bill with prominent tomial serrations and rather short, rounded tail are characteristic of genus. Male of nominate has frontlet violet, rest of upperparts dark bronzy-green, tinged dark bronze on nape; uppertail-coverts blue with duller tips, tail blue-black; underparts blue-black glossed with bluish green on throat and breast. Female with frontlet greenish blue, otherwise like male; lateral rectrices tipped with dull grey; underparts dull, greyish bronzy-green. Race *guianensis* differs in paler ventral colouring, less intensely violet forecrown of

male, and shorter bill. In female, frontlet usually almost or just as large as that of male but may be small or even absent altogether, apparently irrespective of age.

Habitat. In E Andes, prefers wet forests of lower mountain slopes, foothills and adjacent lowlands, especially in broken terrain with dark ravines, gorges and rocky outcrops; usually from mid-strata to lower canopy in forest but may descend to shrub level along forest edges and (females) to nest. At 400-1600 m in Colombia, most abundant at 800-1200 m. Race *guianensis* occurs disjunctly in upper tropical-subtropical forests on tepuis (table mountains), and not reported from intervening areas.

Food and Feeding. Hovers to visit hanging, tubular flowers of epiphytic Ericaceae (*Satyria*, *Psammisia*), Loranaceae (*Psittacanthus*) as well as horizontally oriented flowers of Rubiaceae, Gesneriaceae and other Ericaceae in lower canopy, along forest streams and at forest edge; not known to defend feeding territories at flowers. Regularly flycatches from perches in lower canopy, forest edge, tops of small trees, and along streams; may hover over streams making repeated dashes for prey in swarms of gnats, also (especially female) hover-gleans foliage and moss along streams.

Breeding. In E Ecuador, nest with 2 eggs Jul; one female in C Colombia with enlarged follicles in Sept. Only described nest E Ecuador. ■ cylindrical structure of moss and cobweb with nest cup at top, suspended from rock overhang in cave. No further information.

Movements. No information available; presumably sedentary, but may show some seasonal altitudinal movements.

Status and Conservation. Not globally threatened. CITES II. Its preferred foothill elevations have been severely deforested over much of Colombian range. Uncommon to fairly common in good forest habitat, but will tolerate some disturbance and occurs in selectively logged and fragmented forest and old secondary forest, albeit at lower abundance, along the Andes; common in cocoa plantations in Nariño (S Colombia). No information available on abundance of *guianensis*, but presumably not threatened, as considerable portions of habitat remain mostly intact; occurs in Imataca Forest Reserve (Venezuela).

Bibliography. Barrowclough *et al.* (1995), Butler (1979), Chubb (1916), Gilliard (1941), González (1998), Grantsau (1988), Hilty & Brown (1986), Mayr & Phelps (1967), Meyer de Schauensee (1949, 1964), Meyer de Schauensee & Phelps (1978), Ruschi (1974, 1986), Salaman & Mazariegos (1998b), Sick (1993), Snow & Gochfeld (1977), Snyder (1966), Stotz *et al.* (1996), Willard *et al.* (1991), Zimmer (1950a).

Genus *CAMPYLOPTERUS* Swainson, 1827

38. Scaly-breasted Hummingbird

Campylopterus curvipennis

French: Colibri de Cuvier **German:** Schuppenbrustkolibri **Spanish:** Colibrí de Cuvier
Other common names: Cuvier's Sabrewing, Cuvier's (Scaly-breasted) Hummingbird; Robert's Hummingbird (*roberti*)

Taxonomy. *Trochilus Cuvierii* DeLatte and Bourcier, 1846, east-central Panama.

Traditionally segregated in genus *Phaeochroa*, but the thickened, flattened shaft of the outer primary in adult male of this species is similar to that of other *Campylopterus*, and the coloration, behaviour and vocalizations of some of the dull-coloured, sexually monochromatic species of that genus also resemble present species. Race *roberti* sometimes given species status, based upon differences in bill and rectrix colour. Six subspecies normally recognized.

Subspecies and Distribution.

C. c. roberti (Salvin, 1861) - extreme SE Mexico, N Guatemala and Belize S on Caribbean slope to NE Costa Rica.

C. c. maculicauda (Griscom, 1932) - Pacific slope of Costa Rica.

C. c. furvescens Wetmore, 1967 - Pacific slope of W Panama.

C. c. saturator (Hartert, 1901) - Coiba I (Panama).

C. c. cuvierii (DeLatte & Bourcier, 1846) - E & C Panama.

C. c. berlepschi (Hellmayr, 1915) - coastal region of N Colombia.



Descriptive notes. 11.5-13 cm; male 10-1 g and female 8-6 g in *maculicauda*, male 9-3 g and female 7-9 g in nominate *cuvierii*. Mostly bronzy-green, with dull buffy borders on feathers of most of underparts imparting ■ scaly appearance; belly greyish-buff; corners of tail dull white, set off by diagonal blackish band from rest of bronzy tail. Female has longer bill on average but otherwise smaller than male, and does not differ in colour. Young bird lacks the thickened shafts of the outer primaries and has prominent buffy fringes on the feathers of the crown, nape and uppertail-coverts. Basal half of lower mandible

pinkish in most races, black in *roberti*; race *saturator* largest and darkest, nominate smallest and palest; *berlepschi* has belly more rusty, white on lateral rectrices more extensive; in *roberti* these rectrices are entirely black except for white tips; *maculicauda* has somewhat greener throat and more extensive black on outer rectrices; *furvescens* has throat and upper breast slightly darker green, belly paler.

Habitat. Dry forest, edges and clearings of gallery forest and humid forest, mangrove, second growth and scrub, fencerows, gardens and other more or less open habitats; avoids interior of closed evergreen forest. In dry forest and mangrove occurs from understorey to mid-strata, and to tree tops along edges. Mainly in lowlands but locally to 1200 m in SW Costa Rica.

Food and Feeding. Visits flowers of trees (*Genipa*, *Hibiscus*, *Pelliciera*, *Inga*, *Erythrina*), shrubs, terrestrial bromeliads (*Bromelia*) etc., for nectar, sometimes perching to probe large blooms; very aggressive, often territorial at rich feeding areas where dominant over smaller hummingbirds. Frequently flycatches from perches, also gleans foliage and bark of trees and shrubs for arthropods.

Breeding. Mainly during rainy season, May-Dec (Guatemala), May-Jan (Costa Rica). Nest a well-built cup of plant down and spiderweb, sometimes with fungal rhizomorphs, heavily decorated on outside with moss and lichen and often with lichen in lining; typically saddled on horizontal branch of small tree 2-8 m above ground. During breeding season males often in loose leks of up to 8 in canopy of second growth or low mangrove, or at forest edge. Clutch size 2; incubation 17-19 days; fledging period 22-26 days (to 29 days in inclement weather conditions); fledglings fed for up to 39 days after leaving nest.

Movements. Basically sedentary, but with more or less pronounced local movements in response to changes in flowering.

Status and Conservation. Not globally threatened. CITES II. Uncommon to locally common in most areas. Probably benefits from forest clearance in most areas, though some mangrove populations may be threatened by loss of habitat due to cutting of mangroves for shrimp culture, etc., especially in Central America. Occurs at Bonampak and Yaxchilán in N Chiapas (S Mexico), in Corcovado National Park and Carara Biological Reserve (Costa Rica), and on Atlantic side of Canal Area (Panama).

Bibliography. Anon. (1992a, 1998a), Hilty & Brown (1986), Howell, S.N.G. (1989a), Howell, S.N.G. & Webb (1995a), Howell, T.R. (1957), Land (1970), Monroe (1968), Olson (1997), Ridgely & Gwynne (1989), Ridgway (1911), Skutch (1964b, 1972, 1981), Slud (1960, 1964, 1980), Smith (1966), Stiles (1985c), Stiles & Skutch (1989), Stiles & Wolf (1970), Stotz *et al.* (1996), Wetmore (1957a, 1968a), Wolf (1970).

39. Wedge-tailed Sabrewing

Campylopterus curvipennis

French: Campyloptère pampa **German:** Blaukron-Degenflügel **Spanish:** Colibrí Ruiseñor
Other common names: Curve-winged Hummingbird/Sabrewing (*curvipennis*); Long-tailed/Tuxtla Sabrewing (*excellens*)

Taxonomy. *Trochilus curvipennis* Lichtenstein, 1830, Mexico.

In past, sometimes separated in genus *Pampa*. Race *excellens* considered by some to be full species; research required in zone of hypothetical contact. Race *pampa* has also been treated as separate species, based mainly on shorter bill, but behaviour and voice similar to those of nominate. Subpopulation of Yucatán Peninsula sometimes regarded as race *yucatanensis*, but doubtfully distinct. Three subspecies currently recognized.

Subspecies and Distribution.

C. c. curvipennis (Lichtenstein, 1830) - SE San Luis Potosí and SW Tamaulipas to N Oaxaca (SE Mexico).

C. c. excellens (Wetmore, 1941) - Sierra de Tuxtla (S Mexico).

C. c. pampa (Lesson, 1832) - Yucatán Peninsula S to N Guatemala and Belize; E Honduras.



Descriptive notes. 12-14 cm; male 9-2-12-7 g, female 5-9-8 g. Male has slightly decurved black bill; crown iridescent bluish-violet to purplish, rest of upperparts metallic green, postocular spot white; underparts grey; outer three primaries with thickened and flattened shafts, strongly decurved; tail long, graduated, bluish green. Female similar to male, shafts of primaries less prominent; tail shorter, less graduated, tipped white on outer rectrices. Immature resembles adult female with buffy feather tips. Race *excellens* is larger, with underparts paler and tail longer; *pampa* has shorter bill, darker grey below.

Habitat. Edges of humid to semi-arid evergreen forest, second growth open woodlands, and flowering gardens from sea-level to 1400 m, most commonly below 300 m. Forages in low to high strata.

Food and Feeding. Takes nectar and arthropods. No information on specific plants visited. Territorial.

Breeding. Little information available. Males in breeding condition have been reported Sept-May (*excellens*).

Movements. Sedentary with some apparent altitudinal movements.

Status and Conservation. Not globally threatened. CITES II. Locally common; seems to accept man-made habitats like edges of flowering gardens; not recorded near agricultural areas. Present at Gómez Fariás (Tamaulipas), El Naranjo (San Luis Potosí), Coatepec and Amatlán (Veracruz), Valle Nacional (Oaxaca), Palenque and Bonampak (N Chiapas) and Chichén Itzá (Yucatán). Race *excellens*, if considered full species, classified as Near-threatened and restricted-range species; present in Los Tuxtlas and Uxpanapa EBA.

Bibliography. Anon. (1998a), Edwards & Tashian (1959), Feinsinger (1976), Friedmann *et al.* (1950), González-García (1993), Howell & Webb (1995a), Johnsgard (1997), Klaas (1968), Land (1970), Lowery & Dalquest (1951), Monroe (1968), Nocolad (1981), Ridgway (1911), Russell (1964), Rutgers & Norris (1972), Smith (1966), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Stresemann (1954), Wetmore (1941, 1943), Winker, Ramos *et al.* (1992).

40. Grey-breasted Sabrewing

Campylopterus largipennis

French: Campyloptère à ventre gris **German:** Graubrust-Degenflügel **Spanish:** Colibrí Pechigrís
Other common names: Bronze-shafted/Tail-coated Sabrewing

Taxonomy. *Trochilus largipennis* Boddaert, 1783, Cayenne.

Four subspecies recognized.

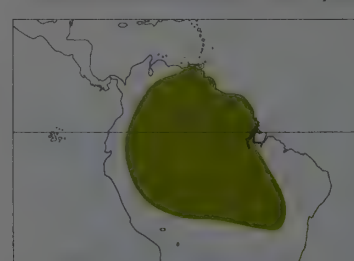
Subspecies and Distribution.

C. l. aequatorialis Gould, 1861 - E Colombia, E Ecuador, E Peru and N Bolivia to NW Brazil.

C. l. largipennis (Boddaert, 1783) - E Venezuela, the Guianas and R Negro region of NW Brazil.

C. l. obscurus Gould, 1848 - E Pará and Maranhão (NE Brazil).

C. l. diamantinensis Ruschi, 1963 - Serra Espinhaço in Minas Gerais (SE Brazil).



Descriptive notes. 13-14.9 cm; male 9-10 g, female c. 8 g. Male has slightly decurved bill, upper mandible black, lower fleshy with black tip; upperparts dark shining green, postocular spot white; underparts uniform dark grey, shafts of outer three primaries thickened and flattened; tail graduated, central pair of rectrices green, remainder bluish black, distal half white. Female similar to male, shafts of primaries less prominent. Immature resembles adult female. Race *obscurus* is smaller, rectrices tipped grey; *aequatorialis* has only last portion of rectrices tipped white; race *diamantinensis* has outer rectrices larger, bronzy-green.

Habitat. Humid forest, second growth, clearings, plantations and thickets at 100-400 m; race *diamantinensis* has been recorded between 1200 and 1400 m. Forages at low to medium heights.

Food and Feeding. Feeds on nectar of flowering Ericaceae, *Heliconia* and other plants; in Nariño (S Colombia), feeds on bushes of Melastomataceae. Arthropods are caught in the air by hawking. Territorial.

Breeding. Birds in breeding condition in Jun (Colombia); one nest in Apr (Brazil). Cup-shaped nest is built out of moss, lined with soft seed material, exterior decorated with large pieces of lichen; saddled on horizontal branch or glued to hanging twigs near waterfalls, or in bushes low above running water. Clutch size 2; incubation and fledging periods unknown.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Uncommon to locally common. Accepts man-made habitats and other disturbed areas like plantations and clearings. Regularly

recorded at Imataca Forest Reserve (Venezuela); also at Timberhead Lodge (N Guyana); and at Tingo María (C Peru).

Bibliography. Balchin & Toyne (1998), Berlioz (1931b, 1964), Bond & Meyer de Schauensee (1943), Cotton (1998a), Friedmann (1948), Gounelle (1909), Grantsau (1988), Haverschmidt & Mee (1994), Hilty & Brown (1986), Meyer de Schauensee & Phelps (1978), Niethammer (1953), Ruschi (1950a, 1963b, 1964e, 1964f, 1973d, 1981-1982, 1986), Rutgers & Norris (1972), Salaman & Mazariegos (1998a, 1998b), Sick (1993, 1997), da Silva (1990), Stotz, Fitzpatrick *et al.* (1996), Stotz, Lanyon *et al.* (1997), Thérý (1987), Tostain *et al.* (1992), Willis (1976), Zimmer (1950b).

41. Rufous Sabrewing

Campylopterus rufus

French: Campyloptère roux

Spanish: Colibrí Rojizo Mexicano

German: Buntschwanz-Degenflügel

Taxonomy. *Campylopterus rufus* Lesson, 1840, no locality = Guatemala.

In past, sometimes separated in genus *Platystylopterus*. Possibly forms superspecies with *C. hyperythrus*. Monotypic.

Distribution. Pacific slope of Mexico (E Oaxaca, Chiapas), S Guatemala and El Salvador.



Descriptive notes. 12-5-14 cm; male c. 9 g, female 6-6-6-9 g. Male has medium-sized, slightly decurved black bill; upperparts iridescent bronzy-green, postocular spot white; underparts uniformly cinnamon; tail slightly rounded, central pair of rectrices golden-bronze, others light cinnamon with black subterminal band, edged cinnamon, outermost tail feather cinnamon with lighter edges. Female similar to male, smaller. Immature like adult, head feathers with buffy fringes.

Habitat. Rainforest and forest edge, canyons with scattered woods, humid pine-oak forests, plantations; occurs at 900-2000 m, occasionally fairly low in dense understorey and in semi-open terrain.

Food and Feeding. Nectar of flowering *Plantago*, *Erythrina*, *Salvia*, *Castilleja*. Insects are caught in the air by hawking. Male occupies feeding territories at nectar-rich sources.

Breeding. Apr-May (Oaxaca, Mexico). Male forms small leks. Cup-shaped nest of moss lined with whitish thistle down, externally decorated with lichen, rather exposed on horizontal branch, 1-2 m above the ground. Clutch size 2; incubation 15-16 days, by female; chick blackish with two rows of buffy dorsal down; fledging 23-26 days.

Movements. Sedentary, with local altitudinal wandering depending on flowering season.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in North Central American Highlands EBA. Locally common. Readily accepts man-made habitats such as plantations or pastures with scattered shrubs and trees. Present at El Triunfo Biosphere Reserve (S Chiapas).

Bibliography. Anon. (1998a), Berlioz (1931b), Binford (1989), Dearborn (1907), Dickey & van Rossem (1938), Friedmann *et al.* (1950), Howell & Webb (1995a), Land (1970), Rowley (1984), Stotz *et al.* (1996), Thurber *et al.* (1987).

42. Rufous-breasted Sabrewing

Campylopterus hyperythrus

French: Campyloptère rougeâtre

Spanish: Colibrí Rojizo Venezolano

German: Rostbauch-Degenflügel

Other common names: Tepui Sabrewing

Taxonomy. *Campylopterus hyperythrus* Cabanis, 1848, Mount Roraima.

Possibly forms a superspecies with *C. rufus*. Often considered conspecific with *C. duidae*. Monotypic.

Distribution. Pantepui, on isolated table mountains in SE Venezuela and adjacent NW Brazil.

Descriptive notes. 12 cm; 5-6-5 g. Male has straight black bill; upperparts shining bronze-green, greener on head; underparts uniform cinnamon, shafts of outer three primaries thickened and flattened; four central tail feathers golden-bronze, outer ones cinnamon-rufous. Female similar to male. Immature resembles adult.

Habitat. Scrub on summits of low tepui (table mountains), highland saxicolous biomes, evergreen high tepui forests and upper montane forests at 1200-2050 m.

Food and Feeding. Forages alone on nectar and tiny arthropods in forest understorey and mid-strata.



Sánchez (1995), Sick (1993, 1997), Stattersfield *et al.* (1998), Stotz *et al.* (1996).

Breeding. No information available.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Tepuis EBA. Although endemic to tepuis of Guayanian region it is a common species in those habitats and no immediate threat is known at present.

Bibliography. Bleiweiss (1990), Dunning (1982), Forrester (1993), Gilliard (1941), Grantsau (1988), Mayr & Phelps (1971), Medina (1992), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Olrog (1968), Phelps & Phelps (1958), Renjifo *et al.* (1997), Ruschi (1964f, 1981-1982, 1986),

43. Violet Sabrewing

Campylopterus hemileucurus

French: Campyloptère violet

German: Violettdegenflügel

Spanish: Colibrí Morado

Other common names: De Lattre's Sabrewing

Taxonomy. *Trochilus hemileucurus* Lichtenstein, 1830, Mexico.

Two subspecies recognized.

Subspecies and Distribution.

C. h. hemileucurus (Lichtenstein, 1830) - S Mexico patchily to SC Nicaragua.

C. h. mellitus Bangs, 1902 - Costa Rica and W Panama.



Descriptive notes. 13-15 cm; male 11-8 g, female 9-5 g. Bill black, more strongly decurved in female. In adult male shafts of outer two primaries strongly thickened, curved and flattened; much less so in adult female and young male and not at all in young female. Head, upper back and underparts of male violet-blue in nominate race, violet in *mellitus*; lower back dark green, broad tail with white outer edges. Female has dark green upperparts, grey underparts with violet gorget, tail as male. Young bird has prominent, dull buffy fringes to feathers of upper- and underparts; lacks violet; rectrices narrower and more pointed than those

of adult; young male dusky bluish-green below.

Habitat. Understorey and edges of humid forest in foothills and on mountain slopes, old second growth, forest patches in disturbed areas, gardens and small banana plantations near forest or woodland; female prefers ravines, and banks of rivers and streams for nesting. Mostly at 100-1500 m (S Mexico), 900-2400 m (Costa Rica, Panama).

Food and Feeding. Visits flowers mainly in understorey, especially *Heliconia*, also those of shrubs like *Cephaelis*, *Palicourea* (Rubiaceae) and banana (*Musa*), including ornamental species like *M. coccinea*. Male occasionally territorial at flowers, but on the whole less aggressive and dominant than large size might suggest. Forages for arthropods more by gleaning foliage and spiderwebs than by flycatching, taking many spiders as well as Diptera, Hymenoptera, etc.

Breeding. Mainly in rainy season, Jun-Sept (S Mexico), May-Oct (Costa Rica), Jul (El Salvador). Nest a bulky, well-constructed cup, mainly of green moss lined with fine fibres and plant down and held together with cobweb, placed on low, slender horizontal branch of small tree or bamboo, typically overhanging stream or ravine, 1-6 m above ground or water. During breeding season up to 10-12 males form leks. No further information.

Movements. Pronounced altitudinal movements in many areas, descending to lower elevations (locally to sea-level) outside breeding season.

Status and Conservation. Not globally threatened. CITES II. Common in many areas, and able to withstand much disturbance as long as some forest cover or tall second growth remains; can use remnant strips of forest along streams as corridors for local movements. Protected areas within range include Las Tuxtlas Biological Station in Mexico (*hemileucurus*), Monteverde Forest Preserve and several national parks in Costa Rica (*mellitus*).

Bibliography. Brown & Bowers (1985), Dickey & van Rossem (1938), Feinsinger (1976, 1977, 1980), Friedmann *et al.* (1950), Howell, S.N.G. & Webb (1995a), Howell, T.R. (1964), Hutto (1985), Johnsgard (1997), Lowery & Dalquest (1951), Monroe (1968), Navarro (1986), Ridgely & Gwynne (1989), Ridgway (1911), Skutch (1967), Slud (1964), Stiles (1979, 1985b), Stiles & Skutch (1989), Stotz *et al.* (1996), Tashian (1952), Thurber *et al.* (1987), Wagner (1946a, 1957b), Wetmore (1968a), Worth (1942).

PLATE 48

inches 2
cm 5



44. White-tailed Sabrewing

Campylopterus ensipennis

French: Campyloptère à queue blanche

Spanish: Colibrí Coliblanco

German: Weißschwanz-Degenflügel

Taxonomy. *Trochilus ensipennis* Swainson, 1822, no type locality given. Monotypic.

Distribution. NE Venezuela, in Cordillera de Caripe and mountains of Paria Peninsula; Tobago. Occurrence on Trinidad questionable; at present no definite records, and specimens collected in 1860, labelled "Trinidad" without exact locality data, may simply represent trade skins obtained on the island.



Descriptive notes. c. 13 cm; male 9.5-10.5 g, female presumably lighter. Male has black decurved bill; upperparts glittering green, postocular spot white; underparts glittering green with throat blue iridescent dark violet; shafts of outer three primaries thickened and flattened; tail squared, central rectrices dark bronzy-green, outer three tail feather pairs proximally black, distal two-thirds white. Female similar to male but underparts pale grey with green discs on flanks. Immature resembles adult female.

Habitat. Montane forest, old second growth, tree-fall gaps, and plantations, at 400-2000 m.

Forages in low and middle strata.

Food and Feeding. Feeds on nectar of flowering bromeliads, *Heliconia*, *Palicourea* and banana (*Musa*). Insects are caught in the air by hawking, typically from a number of adjacent perches; territorial, though recent work suggests territories are related to breeding, not feeding.

Breeding. Two nests on Tobago in Feb; nest cup-shaped, large, made mainly of moss, saddled on horizontal branch, in fork, or attached to ends of hanging twigs; in shrubs, 1.7-2.5 m above ground or running water. Clutch size 2; incubation by female. No further information.

Movements. No information. Some altitudinal dispersal most likely.

Status and Conservation. VULNERABLE. CITES II. Restricted-range species; present in Caripe-Paria Region EBA. Rare to locally common. Habitat destruction is main threat. On Tobago, population suffered severely from 1963 hurricane "Flora" which destroyed most of the forest on the island, with only small patches remaining; only a few individuals recorded in 1974/75 that survived in remaining forest area; today forest is slowly regenerating and population on Tobago seems to be stable or slightly increasing. In Venezuela, deforestation of suitable habitat for agricultural purposes is main threat; slash-and-burn destruction for cash-crop cultivation occurs widely. Although seems to accept slightly disturbed areas like coffee plantations, has never been recorded in strictly agricultural areas. Only some remote forest patches are still pristine, mainly on E end of Paria Peninsula; these patches are presently threatened by a pipeline project across the peninsula known as "Proyecto Colón". Occurs in Paria Peninsula National Park, where fairly common, and recorded density in this region is at least 1.5 pairs/km²; also occurs in Cueva del Guácharo National Park, where is apparently one of the commoner birds, present all year.

Bibliography. Anon. (1989b), Belcher & Smoother (1936), Berlioz (1931b), Bond *et al.* (1989), Chapman (1925b), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), French (1991), Hayes (1996), Hayes, Bullard *et al.* (1995), Hayes, Garnett, Bernard, Bullard *et al.* (1997), Hayes, Garnett, Bernard & Samad (1997), Herklots (1961), Jouanin (1946), Junge & Mees (1958), Meyer de Schauensee & Phelps (1978), Murphy (1991), Paynter (1982), Phelps & Phelps (1958), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Thelen & Faizol (1980), Wege & Long (1995).

45. Lazuline Sabrewing

Campylopterus falcatus

French: Campyloptère lazulite

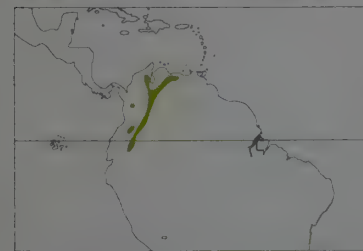
German: Rotschwanz-Degenflügel

Spanish: Colibrí Lazulita

Taxonomy. *Trochilus falcatus* Swainson, 1821, northern Venezuela.

In past, sometimes placed in genus *Saeptiopterus*. Monotypic.

Distribution. Coastal ranges of NC Venezuela down E slope of Andes to NE Ecuador.



Descriptive notes. 11.5-13 cm; c. 7.6 g. Male has black decurved bill; upperparts glittering green, blue on crown; throat and breast glittering dark violet-blue shading to glittering blue, green on belly, shafts of outer three primaries thickened and flattened; tail feathers chestnut, central pair broadly tipped bronze-green. Female similar to male, also with white postocular spot; throat glittering bluish, rest of underparts plain grey, flanks with green discs, tail similar to that of male but often with more green on central rectrices. Immature resembles adult female.

Habitat. High and low montane semi-deciduous forest, flowering gardens, plantation edges and sub-*páramo*, at 900-3000 m.

Food and Feeding. Feeds on nectar of flowering Ericads, *Heliconia*, *Hibiscus* and other flowers. Arthropods are caught in the air and gleaned from foliage. Forages in understorey and mid-strata of forest. Reported to drink water stored in *Heliconia* bracts.

Breeding. Birds in breeding condition in June, Perijá mountains, Colombia/Venezuela. No further information.

Movements. No precise information; presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Uncommon and patchily distributed in montane evergreen forests of N Andes. Relatively sensitive to some habitat changes, but readily accepts man-made habitats like flowering gardens and plantations. Occurs at Colonia Tovar, near Caracas (N Venezuela); also near San Andrés de Pisimbalá (SC Colombia).

Bibliography. Best *et al.* (1997), Bleiweiss (1990), Butler (1979), Chapman (1926), Dunning (1982), Ejlsdál & Krabbe (1990), Hilty & Brown (1986), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Miller (1952), Olog (1968), Phelps & Phelps (1958), Rutgers & Norris (1972), Sánchez (1995), Stotz *et al.* (1996).

46. Santa Marta Sabrewing

Campylopterus phainopeplus

French: Campyloptère des Santa Marta

Spanish: Colibrí de Santa Marta

German: Santa-Marta-Degenflügel

Taxonomy. *Campylopterus phainopeplus* Salvin and Godman, 1879, Santa Marta Mountains, Colombia.

In past, sometimes placed in genus *Saeptiopterus*. Monotypic.

Distribution. NE & S slopes of Santa Marta Mts (NE Colombia).



Descriptive notes. c. 13 cm. Male has slightly decurved black bill; upperparts glittering emerald-green, postocular spot white, face black; throat and breast iridescent blue, rest of underparts dark green, shafts of outer three primaries thickened and flattened; tail squared, dark steely blue. Female upperparts shining green; below greyish-white with green flanks and undertail-coverts; tail mainly green with outer rectrices tipped greyish. Immature resembles adult female.

Habitat. Borders of humid forest, plantations, especially old banana plantations, sometimes in bushy *páramo* up to snow-line, at 1200-4800 m.

m. Forages in lower strata.

Food and Feeding. Takes nectar and insects; no specific food plants recorded, except flowering banana (*Musa*); territorial.

Breeding. Birds in breeding condition Apr-Jun, displaying males Jun-Jul. No further data available.

Movements. Seasonal altitudinal movements at lower elevations (1200-1800 m) during dry season (Feb-May), higher, occasionally up to snow-line (4800 m), during wet season (Jun-Oct).

Status and Conservation. Not globally threatened. CITES II. Currently considered Near-threatened. Restricted-range species; present in Santa Marta Mountains EBA. Locally common but restricted in range. Readily accepts man-made habitats like banana plantations. Most of distributional range cannot be visited safely resulting in lack of life-history data.

Bibliography. Berlioz (1931b), Ejlsdál & Krabbe (1990), Hilty & Brown (1986), Meyer de Schauensee (1982), Olog (1968), Renjifo *et al.* (1997), Salaman & Mazariegos (1998a), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Todd & Carriker (1922).

47. Napo Sabrewing

Campylopterus villaviscensio

French: Campyloptère du Napo

German: Napodegenflügel

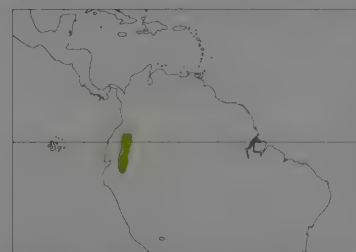
Spanish: Colibrí del Napo

Other common names: Splendid/Villaviscensio Sabrewing

Taxonomy. *Trochilus Villaviscensio* Bourcier, 1851, Napo, Ecuador.

In past, sometimes placed in genus *Saeptiopterus*. Monotypic.

Distribution. Tropical and subtropical S Colombia, E Ecuador and NE Peru.



Descriptive notes. c. 13.5 cm; male 7.4-9.3 g, female 5.2-7.4 g. Male has almost straight black bill; crown glittering golden green, postocular spot white, rest of upperparts bronzy-green; throat and chest dark violet-blue, rest dark grey with green discs, shafts of outer three primaries thickened and flattened; tail slightly forked, dark blue, with central rectrices bronze-green. Female emerald-green above; underparts grey; tail forked, blue-green, outer rectrices tipped whitish-grey. Immature resembles adult female.

Habitat. Montane humid forest at 1000-1800 m; found at 780 m in Nariño (S Colombia). Forages in low to medium strata.

Food and Feeding. Feeds on nectar, presumably of flowering *Heliconia*, bromeliads and other plants; insects are caught in the air by hawking.

Breeding. Birds in breeding condition Oct-Nov; no further data available.

Movements. Unknown.

Status and Conservation. Not globally threatened. CITES II. Currently considered Near-threatened. Restricted-range species; present in Ecuador-Peru East Andes EBA. Locally common but habitat partly under threat of deforestation; does not seem to accept man-made habitats. Regularly recorded on Loreto road between Tena and Coca (NE Ecuador). Only recently (1998) discovered to occur in S Colombia, in Nariño and Putumayo. Research required.

Bibliography. Bulchin & Toyne (1998), Berlioz (1931b), Best *et al.* (1997), Butler (1979), Davis (1986), Meyer de Schauensee (1966, 1982), Olog (1968), Salaman & Mazariegos (1998a, 1998b), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Zimmer (1950b).

48. Buff-breasted Sabrewing

Campylopterus duidae

French: Campyloptère montagnard

German: Tepuidegenflügel

Spanish: Colibrí del Duida

Other common names: Duida Sabrewing

Taxonomy. *Campylopterus duidae* Chapman, 1929, Mount Duida, Venezuela.

In past, sometimes placed in monospecific genus *Loxopterus*. Often considered conspecific with *C. hyperythrus*. Proposed race *zuloagae* (S Venezuela) is considered a synonym of nominate. Two subspecies recognized.

Subspecies and Distribution.

C. d. guaiquinimae Zimmer & Phelps, 1946 - Mt Guaiquinima (S Venezuela).

C. d. duidae Chapman, 1929 - S Venezuela and adjacent N Brazil.



Descriptive notes. 12 cm. Very similar to *C. hyperythrus*; male has straight black bill; upperparts shining bronze-green, greener on head; underparts drab, tinted with tawny on sides, shafts of outer three primaries thickened and flattened; outer tail feathers have dull bronze basal portion. Female similar to male. Immature resembles adult female. Race *guaiquinimae* differs slightly in tone of upperparts, and in darker tail.

Habitat. In forested foothills and lower evergreen montane forests, and in low and high tepui (table mountain) scrub at 1220-1700 m.

Food and Feeding. Forages on nectar and tiny

spiders and insects in forest understorey and mid-strata.

Breeding. Nests placed 2-3 m above the ground. No further information.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Tepuis EBA. Although endemic to tepuis of Guayanian region it is common in those habitats; no immediate threat recorded.

Bibliography. Barrowclough *et al.* (1995), Bleiweiss (1990), Dunning (1982), Forrester (1993), Grantsau (1988), Mayr & Phelps (1967), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Oltrog (1968), Phelps & Phelps (1958), Renjifo *et al.* (1997), Ruschi (1964f, 1981-1982, 1986), Sánchez (1995), Sick (1993, 1997), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Willard *et al.* (1991), Zimmer & Phelps (1946).

49. Sombre Hummingbird

Campylopterus curvipennis

French: Colibri vert et gris

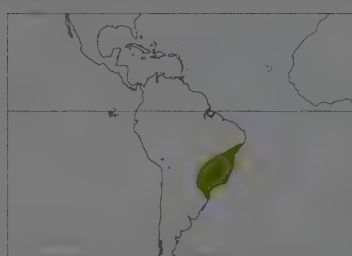
German: Erzkolibri

Spanish: Colibrí Apagado

Taxonomy. *Trochilus curvipennis* Vieillot, 1818. Rio de Janeiro.

Formerly placed in monospecific *Aphantochroa*, but external morphology and flattened and thickened shafts of outer primaries may justify recent placement within *Campylopterus*, though systematic relationships still uncertain. Monotypic.

Distribution. E Brazil, from Goiás and Pernambuco to Mato Grosso and Rio Grande do Sul.



Descriptive notes. c. 12 cm; c. 9 g. Male has slightly decurved black bill; upperparts bronzy-green to blackish bronzy-green, postocular spot white, uppertail-coverts with slight coppery sheen; underparts dull grey, some dull green discs on throat; shafts of outer primaries slightly thickened and flattened; tail squared, central rectrices shiny green, remainder black with some bronzy gloss. Female similar, slightly smaller. Immature resembles adult.

Habitat. Edges and understorey of humid forest, plantations.

Food and Feeding. Feeds on nectar of flowering

er bromeliads, *Heliconia* and other plants. Arthropods caught in the air by hawking.

Breeding. Nov-Mar; nest is cup-shaped, built of soft plant material decorated with large pieces of lichen on the outside, saddled on horizontal branch. Clutch size 2; incubation by female 15-16 days; fledging period 28 days.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Common to locally common throughout its range. Commonly seen along Graciosa Road near Morretes, Paraná, SE Brazil, with density of at least 1-2 pairs/km². Occurs in Serra dos Órgãos and Itatiaia National Parks (Rio de Janeiro) and Parque Estadual da Pedra Talhada (Alagoas).

Bibliography. de Almeida & Ruschi (1976), Belton (1984), Forrester (1993), Gonzaga *et al.* (1995), Grantsau (1988), Oniki (1996), Pacheco *et al.* (1996), Parker & Goerck (1997), do Rosário (1996), Ruschi (1949b, 1964f, 1976d, 1981-1982, 1986), Sargeant (1996), Scott & Brooke (1985), Sick (1993, 1997), Sick & Teixeira (1981), Stotz *et al.* (1996), Tobias *et al.* (1993), Willis (1992).

50. Swallow-tailed Hummingbird

Campylopterus macrourus

French: Colibri hirondelle

German: Blauer Gabelschwanzkolibri

Spanish: Colibrí Golondrina

Other common names: Common/Brazilian Swallowtail, Cayenne Forktailed Hummingbird

Taxonomy. *Trochilus macrourus* J. F. Gmelin, 1788, Jamaica; error = Cayenne.

Formerly placed in monospecific genus *Eupetomena*; shape structure and enlarged shaft of primary in male support present treatment in *Campylopterus*. Nominant and race *simoni* intergrade in C Brazil (C Goiás, W & C Minas Gerais). Five subspecies recognized.

Subspecies and Distribution.

C. m. macrourus (J. F. Gmelin, 1788) - the Guianas and N, C & SE Brazil (Amapá and Pará; Mato Grosso, Goiás and Minas Gerais to São Paulo) to Paraguay.

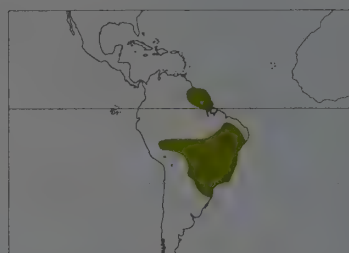
C. m. simoni (Hellmayr, 1929) - NE Brazil (S Maranhão, Piauí, Ceará, Pernambuco and Bahia to C Goiás and C Minas Gerais).

C. m. cyanoviridis (Grantsau, 1988) - SE Brazil (Serra do Mar in S São Paulo).

C. m. hirundo (Gould, 1875) - E Peru (Huiro).

C. m. bolivianus (Zimmer, 1950) - NW Bolivia (Beni).

Descriptive notes. 15-17 cm (including bill of 2.1 cm, tail 7.9 cm); male 8-9 g, female 6-7 g. Male has slightly curved black bill; head, throat and breast deep violet-blue; upperparts and underparts blue-green or shining bronzy-green; tail deeply forked, blue. Female like male but smaller and duller. Immature like female but with brown-tinged feathers on head and neck. Race *simoni* with



bluish green on back and underparts; *hirundo* has head and throat dull cobalt-blue, tail less deeply forked; *cyanoviridis* has head, throat and breast shining blue-green, back and underparts golden bronzy-green; *bolivianus* has head greenish, contrasting with green on back, all colours very clear and bright.

Habitat. Open savanna-like vegetation with shrubs and trees, man-made habitats such as gardens, parks and plantations, also primary forest and forest edges. Common from sea-level to 1500 m. Forages from mid-strata to tree tops.

Food and Feeding. Nectar of native and introduced flowering trees, including Leguminosae, Malvaceae, Bombacaceae, Rubiaceae, Myrtaceae; epiphytic bromeliads and gesneriads. Defends nectar-rich resources. Feeds on insects in the air.

Breeding. Oct-Mar, also Jun in state of São Paulo. Cup-shaped nest is constructed on thin horizontal twigs of shrub or tree, usually at 1-3 m, but nests have also been found high in trees at 10-15 m. Nest material consists of fine plant fibre inside, moss and lichen outside. Clutch size 2; incubation 15-16 days, by female; chick dark with sparse, dark grey dorsal down; fledging 22-24 days; young return to nest during the first few nights and remain with adult female for 2-3 weeks. First breeding in second year.

Movements. Short-distance N-S migrant in Brazil.

Status and Conservation. Not globally threatened. CITES II. Rare in the Guianas. Common resident in Brazil, with densities of at least 3-6 individuals/km² in parks of large cities, such as São Paulo and Campinas; occurs in Serra da Canastra, Serra do Cipó and Brasília National Parks. Ready occupation of man-made habitats suggests that habitat loss is unlikely to be a problem. Trapping for wild-bird trade was significant until 1970 but has now ceased.

Bibliography. Bech *et al.* (1997), Belton (1984), Berlioz (1934), Davis (1993), Dubs (1992), Gobatto & Stort (1992), Grantsau (1988), Gyldenstolpe (1945b), Haverschmidt & Mees (1994), Hayes (1995), Hellmayr (1929), Helme (1996), Laubmann (1933, 1940), Oniki (1996), Parker *et al.* (1982), Remsen & Traylor (1989), do Rosário (1996), Ruschi (1951, 1964f, 1981-1982, 1982a), Rutgers & Norris (1972), Schürer (1983), Short (1975), Sick (1993, 1997), Stotz *et al.* (1996), Tobias *et al.* (1993), Todd (1942), Tostain *et al.* (1992), Zimmer (1950b).

Genus FLORISUGA Bonaparte, 1850

51. White-necked Jacobin

Florisuga mellivora

French: Colibri jacobin

German: Weißnackenkolibri

Spanish: Colibrí Nuquiblanco

Other common names: (Great) Jacobin/White-bellied(!)/Collared Hummingbird

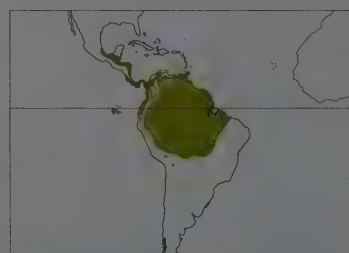
Taxonomy. *Trochilus mellivorus* Linnaeus, 1758. India; error = Surinam.

Over the wide continental range of this species several races have been named, but all are now lumped into nominate; only birds on Tobago, distinguishable by larger size, are generally separated, although some birds from Santa Marta Mts (NE Colombia) are apparently as large. For this race the name *tobagensis* is a frequently used synonym. Two subspecies recognized.

Subspecies and Distribution.

F. m. mellivora (Linnaeus, 1758) - S Mexico to Panama and Colombia, S to W Ecuador, SE Peru and N Bolivia, and E to Venezuela, Trinidad, the Guianas and Amazonian Brazil.

F. m. flabellifera (Gould, 1846) - Tobago.



Descriptive notes. 11-12 cm; male 7-4 g, female 6-5 g. Bill and feet black. Adult male with head and chest blue, broad white crescent on nape; rest of upperparts bright green including elongated uppertail-coverts; belly and most of tail white, narrowly edged and tipped black. Plumage of adult female notoriously variable, apparently individually; perhaps half to two-thirds show the "typical" female plumage with blue-green breast heavily scaled with whitish, belly dull white, upperparts entirely green and tail mostly green with dark blue tip, outer rectrix with white outer edge and tip; the remainder have plumage more or less male-like

with a few only distinguishable from adult male by their longer bills and shorter wings and tails (though overlaps exist in all measurements). Adult female may show plumages resembling those of immature as well as adult male. Proportions of male-like females may also vary geographically; much more study required. In young male, plumage varies from essentially female-like, but with more white in the tail, to male-like with more black in the tail; both female and young male sometimes show buffy stripes on malars and centre of rump; young female similarly variable but usually with less white in tail, often more bronzy on throat and chest. Race *flabellifera* larger.

Habitat. Humid forest canopy and borders, nesting in understorey; semi-open habitats of various types, e.g. lighter woodland, coffee and cacao plantations; tall second growth; and gallery forest. Usually high in trees, lower at edges and clearings. Occurs from sea-level up to c. 900 m; rarely, perhaps seasonally, up to 1500 m or more.

Food and Feeding. Visits flowers of a variety of trees, including *Inga*, *Vochysia*, *Erythrina*, *Bauhinia* and *Symphonia*, epiphytes (*Norantea*, *Columnnea*, bromeliads), shrubs and *Heliconia* along edges and in clearings. Many concentrate at flowering trees, where they are aggressive but infrequently territorial; also at *Heliconia*. Both sexes hawk flies for long periods, hovering and darting high above streams and clearings, or sallying from tree-top perches; less often glean foliage, female sometimes in understorey. Arthropod food mainly small Diptera and Hymenoptera, some individuals recorded taking ants.

Breeding. Dry to early wet seasons: Jan-Jun or Jul in Costa Rica and Panama; Feb-May in NW Colombia, Jun and Nov in E Colombia. Nest a rather shallow soft, felted cup of light-coloured plant down and cobweb, on flat upper surface of broad leaf of understorey palm (*Geonoma*, *Asterogyne*), where sheltered from above by another such leaf, 1-3 m above ground, sometimes near a stream. During breeding season chases and displays by male-plumaged birds noted in canopy and along edges, but not known to form leks. No further information.

Movements. Not well understood. In many areas reported to be common during some seasons, rare to absent in others, but no clear patterns evident on present information. Nominate casual or accidental on Aruba and the Grenadines (Carriacou).

Status and Conservation. Not globally threatened. CITES II. Uncommon to common, at least seasonally, over most of its broad range and appears well able to use disturbed and man-made habitats such as tree plantations. Occurs regularly within many protected areas, including Corcovado National Park (Costa Rica), Los Katíos and Amacayacu National Parks (Colombia), Guatopo and Sierra Nevada National Parks (Venezuela), Asa Wright Nature Centre (Trinidad) and Serra dos Orgãos National Park (Brazil).

Bibliography. Álvarez del Toro (1980), Barrowclough *et al.* (1995), Blake (1958), Bond & Meyer de Schauensee (1943), Brown & Bowers (1985), Cotton (1998a), Elgar (1978), Feinsinger (1980), Feinsinger *et al.* (1985), Iffrench (1991), Figueroa *et al.* (1998), Friedmann (1948), Friedmann *et al.* (1950), Grantsau (1988), Gyldestolpe (1945b), Haverschmidt & Mees (1994), Herklots (1961), Hilty (1997), Hilty & Brown (1986), Howell & Webb (1995a), Johnsgard (1997), Lowery & Dalquest (1951), Meyer de Schauensee & Phelps (1978), Monroe (1968), Nocedal (1981), Pople *et al.* (1997), Ridgely & Gwynne (1989), Ridgway (1911), Ruschi (1949a, 1981-1982, 1986), Rutgers & Norris (1972), Sick (1993, 1997), Slud (1960, 1964), Snow & Snow (1972), Snyder (1966), Stiles (1980, 1985b, 1995b), Stiles & Skutch (1989), Stotz, Fitzpatrick *et al.* (1996), Stotz, Lanyon *et al.* (1997), Tostain *et al.* (1992), Wetmore (1968a), Willis (1976), Zimmer (1950b).

52. Black Jacobin

Florisuga fusca

French: Colibri demi-deuil **German:** Schwarzkolibri **Spanish:** Colibrí Negro

Other common names: Pied/Dusky/White-tailed Jacobin

Taxonomy. *Trochilus fuscus* Vieillot, 1817, Brazil.

Traditionally placed in monospecific *Melanotrochilus*; inclusion in *Florisuga* based on voice, morphology, anatomy and reproductive behaviour. Monotypic.

Distribution. E Brazil (Rio Grande do Norte to Rio Grande do Sul) to SE Paraguay, NE Argentina and N Uruguay.

Descriptive notes. 12-13 cm; male 9 g, female 7 g. Sexes alike; immature plumage has sometimes been erroneously attributed to adult female. Bill straight, black; back and underparts black; lower back, uppertail-coverts and upperwing-coverts shining bronze-olive; flanks white; central tail feathers



black, the rest white tipped black. Immature has broad cinnamon band on sides of throat; feathers on back fringed chestnut; underparts black with varying amount of brown spots, flanks and lower belly white; tail black, except outermost feathers which are white.

Habitat. Frequently found in woodlands, gardens and mixed plantations with tall trees, from sea-level to 1400 m. Forages from lower to upper strata and at forest edge.

Food and Feeding. Searches for nectar at native and introduced shrubs and trees, including *Hibiscus*, *Eugenia*, *Eucalyptus*, *Erythrina*, *Calliandra*, *Dombeya*. In Rio Grande do Sul, in

Jul, congregations of more than 50 individuals have been observed feeding on the pink flowers of *Dombeya wallichii* (Sterculiaceae). Feeds on insects in the air, or gleans from leaves and spider webs.

Breeding. Aug-May. Nest is cup-shaped, of fine plant fibre and cobweb attached to mid-rib of strong large horizontal leaf in shrub or tree at 1-4 m. Clutch size 2; incubation 16-17 days, by female; chick is black with some grey dorsal down; fledging period 22-25 days; young remain with female for 3-4 weeks. Up to 2 broods raised per year. First breeding in second year.

Movements. Migratory. Appears in Rolândia, Paraná, SE Brazil Mar/Apr and leaves Sept; disappears from Rio de Janeiro May/Jun and returns Oct; in Rio Grande do Sul large aggregations of 40 to 60 individuals observed Jul. Phenology of migration pattern poorly understood.

Status and Conservation. Not globally threatened. CITES II. Common resident throughout Brazilian range. Occurs in Itatiaia National Park (Brazil). Ready occupation of man-made habitats suggests that habitat loss is unlikely to be a problem. Trapping for wild bird trade was significant until 1970's but has now apparently ceased.

Bibliography. Bech *et al.* (1997), Belton (1984), Canevari *et al.* (1991), Colmán & Pérez (1991), Flores (1995), Forrester (1993), Grantsau (1988), Hayes (1995), Jouanin (1949), Lamm (1948), Lowen, Clay *et al.* (1997), Mengel (1960), Narosky (1979), Oniki (1996), de la Peña (1994), do Rosário (1996), Ruschi (1952, 1973d, 1981-1982, 1982a, 1982c, 1986), Rutgers & Norris (1972), Sagot (1998b), Saibene *et al.* (1996), Sick (1993, 1997), Snow & Snow (1986), Snow & Teixeira (1982), Steinbacher (1936), Stotz *et al.* (1996), Tobias *et al.* (1993), Willis (1992), Wittmann (1982).



PLATE 49

inches 2
cm 5

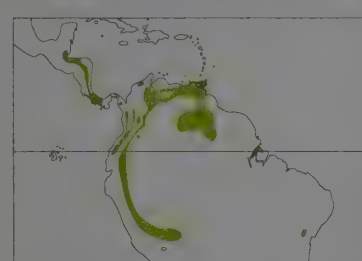
Genus *COLIBRI* Spix, 1824

53. Brown Violet-ear

Colibri delphinae

French: Colibri de Delphine German: Brauner Veichenohrkolibri Spanish: Colibrí Pardo

Taxonomy. *Ornismya Delphinae* Lesson, 1839, no locality = Santa Fé de Bogotá, Colombia. Proposed race *greenwalti* of Bahia (E Brazil), claimed to differ very subtly in coloration, does not appear sufficiently distinct to merit recognition. Monotypic.
Distribution. Guatemala and Belize to Colombia, then S to W Ecuador, E Peru and N Bolivia, and E to Venezuela, Trinidad, Guyana and NC Brazil (Roraima); E Brazil (Serra Sincorá in Bahia).



Descriptive notes. 11-12 cm; male 6-9 g, female 6-1 g (Costa Rica). Sexes similar in coloration but male averages larger in all dimensions except bill length. Adult mainly dull greyish brown, glossed with green on the back; uppertail-coverts dusky, broadly edged with cinnamon; tail bronze-green with greenish black subterminal band, narrow ochraceous to greyish tip; violet patch from below eye to auriculars; lores and broad malar stripe buffy-white; centre of throat glittering green, to blue at lower edge; bill black, feet dark grey. Young bird differs from adult in showing broad cinnamon-buff to dull rufous borders to most of dorsal feathers and in having the blue-violet auricular patch largely or entirely replaced by darkish grey.

Habitat. Canopy and edges of humid forest, tall second growth, semi-open habitats like coffee plantations and shrubby clearings. Usually high in trees, but descends to shrub level along edges and at gaps and clearings. Prefers hilly country and lower mountain slopes, though descends to adjacent lowlands occasionally or seasonally. Recorded at 100-1600 m (Costa Rica), 100-2800 m (Colombia), 300-2000 m (Venezuela).

Food and Feeding. Visits a variety of flowers, usually those with short corollas (or nectariferous bracts) including those of trees (*Inga*, *Erythrina*, *Calliandra*, *Clusia*, *Warszewiczia*), epiphytes (especially Marcgraviaceae), vines (*Gurania*) and shrubs (*Cephaelis*, *Stachytarpheta*); aggressive, typically dominating smaller hummingbirds, but usually not territorial at flowers. Regularly hawks small flying insects by sallying from perch or hovering and darting high in air at breaks in canopy or low over streams.

Breeding. Late wet and early dry seasons: Nov-May in Costa Rica; Dec-Jan in E Venezuela; Nov and Apr in Colombia. Males form leks in canopy, usually 3-8 males at intervals of 30-60 m along ridgetop or forest edge. Nest a small cup of plant down saddled on twig of small shrub under bamboo, average 1-2 m above ground (Trinidad).

Movements. In most areas breeds mainly above 500-900 m, descending to lower elevations outside breeding season.

Status and Conservation. Not globally threatened. CITES II. Scarce, or at least infrequently recorded, over most of broad range, but locally common in some areas: freely uses altered or man-made habitats like second growth and coffee plantations.

Bibliography. Barrowclough *et al.* (1997), Belcher & Smoother (1936), Bloch *et al.* (1991), Elgar (1977, 1982a), Feinsinger (1976, 1980), ffrench (1991), Grantsau (1988), Haverschmidt & Mees (1994), Herklots (1961), Hilty (1997), Hilty & Brown (1986), Howell & Webb (1992a, 1995a), Junge & Mees (1958), Meyer de Schauensee & Phelps (1978), Monroe (1968), Murphy (1991), Perry *et al.* (1997), Rasmussen *et al.* (1996), Ridgely & Gaulin (1980), Ridgely & Gwynne (1989), Ridgway (1911), Ruschi (1981-1982, 1986), Rutgers & Norris (1972), Sick (1993, 1997), Slud (1960, 1964), Snyder (1966), Stiles (1985b), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968a), Zimmer (1950d).

54. Green Violet-ear

Colibri thalassinus

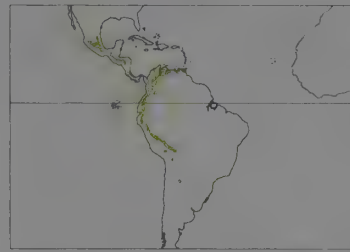
French: Colibri thalassin German: Kleiner Veichenohrkolibri Spanish: Colibrí Verdemar
Other common names: Mexican Violet-ear (*thalassinus*); Mountain Violet-ear (*cyanotus*)

Taxonomy. *Trochilus thalassinus* Swainson, 1827, Tamasalcátepec, state of Mexico, Mexico. The three southern races have sometimes been considered a separate species, *C. cyanotus*. Formerly recognized race *minor* of Honduras and Nicaragua is now usually subsumed into nominate; *cyanotus* and *crissalis* apparently intergrade through Colombia and Ecuador, and their distinctness has been questioned. Four subspecies currently recognized.

Subspecies and Distribution.

- C. t. thalassinus* (Swainson, 1827) - C & S Mexico to NC Nicaragua.
- C. t. cabanidis* (Heine, 1863) - Costa Rica and W Panama.
- C. t. cyanotus* (Bourcier, 1843) - mountains of Venezuela, Colombia and Ecuador.
- C. t. crissalis* Todd, 1942 - Andes of Peru and Bolivia, and extreme NW Argentina.

Descriptive notes. 10.5-11.5 cm; male 5-7 g, female 4-8 g. Plumage mostly a rather bluish green, with subterminal blue-black band on tail and broad violet patch from below eye to auriculars; feathers of throat and chest glittering green with darker centres; undertail-coverts edged with buff; bill and feet black. Male averages larger than female in all measurements except bill length; area of throat and breast with glittering green feathering is brighter and more extensive. Young birds lack the glittering green feathering below, the feathers being bronzy-green with narrow buff fringes; feathers of crown, nape and rump have narrow dull rufous fringes, and violet auricular patch (and that of the chest in nominate) are reduced or absent. Nominat differs from other races in having violet-blue patch on chest, although race *cabanidis* sometimes shows some blue on chest; nominate sometimes has chin blue, and bill is noticeably slimmer; race *crissalis* differs from *cyanotus* in having slightly paler underparts and little or no green in feathers of undertail-coverts, which are nearly uniform pale buff.



Habitat. Open, shrubby mountain slopes and highland pastures with scattered trees, forest edge adjoining highland scrub, landslide scars, streams, penetrating locally into forest understorey; hedgerows, second growth, coffee plantations, shady gardens. In most areas at 1200-3000 m, outside breeding season down to 500-1000 m locally.

Food and Feeding. Visits flowers of a variety of herbs (*Salvia*, *Lobelia*, *Cirsium*), shrubs (*Centropogon*, *Cephaelis*, *Besleria*, *Cuphaea*, *Stachytarpheta*), epiphytes (*Columnnea*, bromeliads), trees (*Inga*, *Clusia*, *Erythrina*), usually foraging at shrub height but perching fairly

high in trees, often overlooking flowers. Aggressive and sometimes territorial at flowers, but often subordinate to hummingbirds of similar or even smaller size. Frequently sallies from high, exposed perches to capture flies and gnats, or may make repeated darts while hovering, usually well above ground; less often gleans foliage at all heights along edges.

Breeding. Mainly late wet to dry seasons, Jul-Nov (C Mexico), Sept or Nov-Mar (Guatemala), Sept-Jan (El Salvador), Oct-Mar (Costa Rica), Mar-Aug (Colombia). During breeding season males sometimes solitary but more often in loose leks of up to 5. Nest a usually subterminal cup of tree-fern scales, plant down, dry grass blades and/or moss, held together with cobweb, lined with soft plant down, and diversely decorated on the outside with bits of bark, moss, lichen or dead leaves, on downward-drooping twig, rootlet, bamboo stem or fern, usually beside some opening like a road, stream or clearing, 1-3 m above ground. Clutch size 2; incubation 16-17 days; fledging period 23-25 days, to 28 days or more in inclement weather.

Movements. No long-distance migrations have been documented, but in most areas moves to lower elevations outside breeding season. Nominat race strays to extreme SW USA.

Status and Conservation. Not globally threatened. CITES II. Locally common to abundant over most of its wide range; has probably benefited from deforestation and habitat alteration in many areas. Present in Volcán Irazú and Volcán Poás National Parks (Costa Rica); also frequently recorded at Tamasalcátepec, Volcán de Fuego, Sierra de Atoyac and Lagos de Montebello (Mexico), Fortuna and Cerro Colorado (Panama), Colonia Tovar, near Caracas (Venezuela), and between Loja and Zamora (Ecuador).

Bibliography. Baepier (1962), Berger (1985), Berlioz (1938), Bertelli *et al.* (1997), Best & Clarke (1991), Bloch *et al.* (1991), Bond & Meyer de Schauensee (1943), Brown & Bowers (1985), Canevari *et al.* (1991), Colwell (1973), Colwell *et al.* (1974), Des Granges & Grant (1980), Dickey & van Rossem (1938), Elgar (1979, 1982a), Feinsinger (1976, 1977, 1980), Feinsinger & Colwell (1978), Fjeldså & Krabbe (1990), Friedmann *et al.* (1950), Gaunt *et al.* (1994), Hilty & Brown (1986), Howell & Webb (1995a), Johnsgard (1997), Lara & Ornelas (1998), Lyster *et al.* (1950), Lyon (1976), Martínez (1989), Meyer de Schauensee & Phelps (1978), Monroe (1968), Moynihan (1979), Olivares (1971), Olrog (1963b), de la Peña (1994), Phelps & Phelps (1958, 1965), Remsen (1985), Remsen, Traylor & Parkes (1986), Ridgely & Gwynne (1989), Ridgway (1911), Salaman & Mazariegos (1998b), Skutch (1967), Slud (1964), Snow & Snow (1980), Stiles (1985b), Stiles & Skutch (1989), Stotz *et al.* (1996), Wagner (1942, 1945, 1957b), Wetmore (1968a), Wolf & Stiles (1970), Wolf *et al.* (1976), Zimmer (1950d).

55. Sparkling Violet-ear

Colibri coruscans

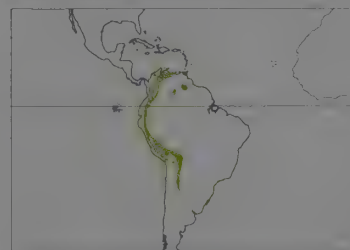
French: Colibri anais German: Großer Veichenohrkolibri Spanish: Colibrí Rutilante
Other common names: Colombian/Gould's/Chequered Violet-ear

Taxonomy. *Trochilus (Petasophora) coruscans* Gould, 1846, South America.

Proposed race *rostratus* (mountains of upper Orinoco Valley) doubtfully distinct from *germanus*; only differences appear to be longer bill and tail. Form "*buckleyi*", known only by type from Bolivia, appears to refer to an aberrant plumage of present species, perhaps the poorly known melanistic form; a reported second specimen from Ecuador may refer to some different form. Two subspecies currently recognized.

Subspecies and Distribution.

- C. c. germanus* (Salvin & Godman, 1884) - S Venezuela, E Guyana and N Brazil.
- C. c. coruscans* (Gould, 1846) - NW Venezuela and Colombia through Ecuador and Peru to Bolivia and NW Argentina; possibly also N Chile.



Descriptive notes. 13-14 cm; male 7-7.8 g, female 6-7.7 g. Male has slightly decurved black bill; upperparts metallic bluish green, bluish violet ear plumes elongated and erect; chin bluish violet, rest of underparts green with blue belly; tail double-lobed, metallic green with steely blue subterminal band. A poorly understood melanistic form exists, but is rare (only 2 amongst over 300 specimens checked). Female similar to male, often has white postocular spot, smaller. Immature has no iridescent coloration, feathers fringed buff. Race *germanus* has forecrown, underparts and tail bluer.

Habitat. Forest edges, open woodland, flowering gardens, plantation, sub-páramo and páramo, at 1700-4500 m.

Food and Feeding. Feeds on nectar of a great variety of flowers like *Castilleja*, *Centropogon*, *Clusia*, *Echeveria*, *Elleanthus*, *Erythrina*, *Eucalyptus*, *Guzmania*, *Inga*, *Salvia*, *Siphocampylus* and *Puya*. Insects are caught in the air by hawking. Forages from ground level to canopy. Territorial, dominates all other hummingbirds at flowering trees; in páramo no aggressive interaction with other hummingbirds observed.

Breeding. Jul-Oct (Venezuela). Cup-shaped nest built of various soft plant materials, decorated outside with lichens and twigs; placed on horizontal branch or attached to pendent twig in bush or placed in cleft in rocks. Incubation 17-18 days, by female; chick dark with two rows of rufous dorsal down; fledging period 20-22 days. Records of males participating in raising young unlikely and need verification. At high altitudes hardly any nestling mortality due to predation.

On following pages: 56. White-vented Violet-ear (*Colibri serrirostris*); 57. Green-throated Mango (*Anthracothorax viridigula*); 58. Green-breasted Mango (*Anthracothorax prevostii*); 59. Black-throated Mango (*Anthracothorax nigricollis*); 60. Veraguas Mango (*Anthracothorax veraguensis*); 61. Antillean Mango (*Anthracothorax dominicus*); 62. Green Mango (*Anthracothorax viridis*); 63. Jamaican Mango (*Anthracothorax mango*); 64. Fiery-tailed Awi-bill (*Anthracothorax recurvirostris*).

Movements. During dry season populations in *páramo* habitats migrate to lower elevation; during this period recorded at altitudes of about 200 m. Populations at lower elevation present all year round, though some may show some seasonal dispersal. Recent record from N Chile (Andes of Tarapacá) in Jul may refer to vagrant, migrant or perhaps a hitherto unknown breeding population.

Status and Conservation. Not globally threatened. CITES II. Common in various habitat types including man-made flowering gardens and plantations, and can be observed in gardens of major cities like Bogotá, Quito and Cuzco. During recent decades has been imported for wild-bird trade into Europe.

Bibliography. de Almeida & Ruschi (1976), Anon. (1982b), Barrowclough *et al.* (1995), Berger (1978, 1985), Best & Clarke (1991), Bloch *et al.* (1991), Böhl (1979), Bond & Meyer de Schauensee (1943), Canevari *et al.* (1991), Carpenter (1976), Chai & Dudley (1995), Dorst (1956), Elgar (1977, 1979, 1982a), Fjeldså & Krabbe (1989, 1990), Gaunt *et al.* (1994), Grantsau (1988), Grummit (1991), Hainsworth (1977), Hellmayr (1932), Hilty (1985), Hilty & Brown (1986), Howell & Webb (1995b), Hüning (1985), Johnson (1967), Koepcke (1970), Kraemer & Schmitt (1991), Marin *et al.* (1989), Meyer de Schauensee & Phelps (1978), Montgomerie & Redsell (1980), Moore (1947a), Moynihan (1979), Munves (1975), Olivares (1963, 1969), de la Peña (1994), Phelps & Phelps (1952), Poley (1980, 1981a), Remsen (1985), Rocha & Peñaranda (1995), Ruschi (1961d, 1964g, 1965c, 1981-1982, 1982a, 1986), Rutgers & Norris (1972), Sallaberry *et al.* (1992), Sanft (1970), Scamell (1966), Schäfer (1954), Schmidt-Marloh & Schuchmann (1980), Schmitt & Schmitt (1987), Schuchmann (1976b, 1983b, 1989), Sick (1993, 1997), Snow (1983), Snow & Snow (1980), Stotz *et al.* (1996), Taczanowski (1884), Warncke *et al.* (1991), Wolf & Stiles (1970), Zimmer (1950d), Züchner (1998).

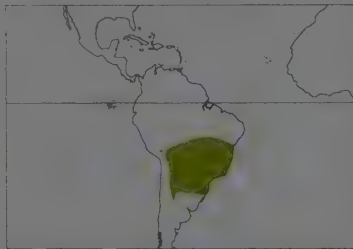
56. White-vented Violet-ear

Colibri serrirostris

French: Colibri à ventre blanc **German:** Amethystohrkolibri **Spanish:** Colibrí Orejmorado
Other common names: Brazilian Violet-ear, Singing Hummingbird

Taxonomy. *Trochilus serrirostris* Vieillot, 1816, Brazil. Monotypic.

Distribution. Bolivia and C Paraguay to S Brazil (from Mato Grosso, Goiás, Bahia and Espírito Santo) and N Argentina (S to Córdoba).



Descriptive notes. 12-13 cm; 5.6-6.8 g. A medium-sized, shining green hummingbird with long, slightly decurved bill; male is lighter green than both *C. coruscans* and *C. thalassinus* with slight differences in coloration of subocular patch and ear-tufts; lower upperparts yellow-green with a blue shimmer; ear-coverts, subocular and postauricular regions spotted violet blue and can be mistaken for a collar. Rectrices glittering green with broad steel-blue subterminal band; undertail-coverts pure white. The upper mandible is sometimes serrated, and bill is same length as head. Female similar to male but slightly smaller, paler and more greyish green. Immature much like female but greyer underneath and greenish brown above, with whitish belly, white malar stripe and white outer corners to tail.

Habitat. Semi-open terrain of several types including scrub, savanna, grassland and bushy gorges. Occasionally in sparse forest. Perches in shrubs and small trees near dense flower patches. Ranges from sea-level (coastal Brazil) to as high as 3600 m (though rarely) in the Andes. Commonest in upland habitat at 1000-1500 m.

Food and Feeding. Very aggressive and territorial, commonly chasing competitors from flower patches. Frequently observed hawking for insects. Dominant birds stay on a nearby perch and call regularly when not feeding at flowers. Usually begins feeding early in the morning compared with other hummingbirds.

Breeding. Dec-Apr. All nest-building, incubation and care of young performed by female. External nest walls decorated with colourful lichens. Clutch 2; incubation 15 days; fledging 22-25 days.

Movements. Some populations make short migrations; birds at higher altitudes in Brazil (above tree-line) migrate to lowland regions in autumn.

Status and Conservation. Not globally threatened. CITES II. Common throughout much of range, particularly at medium altitudes; readily accepts man-made habitats, e.g. gardens and parks. In Brazil, frequently recorded in Itatiaia, Serra da Canastra, Serra do Cipó and Brasília National Parks. Recorded density of at least 1-2 pairs/km² in vicinity of São Paulo.

Bibliography. Alves & Cavalcanti (1996), Antas & Cavalcanti (1988), Belton (1984), Berry (1989), Bond & Meyer de Schauensee (1943), Canevari *et al.* (1991), Davis (1993), Dubs (1992), Elgar (1982a), Fjeldså & Krabbe (1990), Fjeldså & Mayer (1996), Forrester (1993), Grantsau (1988), Hayes (1995), Laubmann (1933, 1940), Oniki (1996), Papi & Ioale (1987), Park & Atyeo (1974), de la Peña (1994), Perry *et al.* (1997), Piratelli (1997), Remsen & Traylor (1989), do Rosário (1996), Ruschi (1949b, 1981-1982, 1982a, 1986), Sargeant (1996), Sazima (1977), Sazima & Sazima (1990), Short (1975), Sick (1993, 1997), Stotz *et al.* (1996), Tobias *et al.* (1993).

Genus ANTHRACOTHORAX Boie, 1831

57. Green-throated Mango

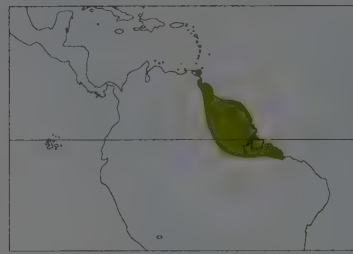
Anthracothorax viridigula

French: Mango à cravate verte **Spanish:** Mango Gorgiverde
German: Smaragdehl-Mangokolibri
Other common names: Green-throated/Black-breasted Hummingbird

Taxonomy. *Trochilus viridigula* Boddaert, 1783, Cayenne.

Probably belongs to the superspecies formed by *A. prevostii*, *A. nigricollis* and *A. veraguensis*. Monotypic.

Distribution. Trinidad, NE Venezuela and the Guianas to N Brazil (Amapá, N Pará, N Maranhão).
Descriptive notes. 10.5-12.5 cm; male 7.5-8.5 g, female 6.0 g; records of 11 g for female are possibly of egg-laying individuals. Male has slightly decurved black bill; upperparts shining bronzy-



green; throat glittering green, centre of breast and belly velvet black, sides green to bronzy-green, thighs and lower sides of body white; central tail feathers dark brown to green, with others shiny purple, outermost ones tipped dark blue. Female bill like male; upperparts similar to male; underparts mostly white with velvet black stripe from chin to belly; tail similar to male's but tipped white. Immature similar to female but sides of chin and underparts chestnut.

Habitat. Coastal regions, including mangrove, marshy savanna and similar open swamp-like habitats with scattered large trees. Forages

mainly in tree tops. Recorded between sea-level and 500 m.

Food and Feeding. Nectar of flowering native and introduced trees, e.g. *Erythrina*, *Caesalpinia*, *Tabebuia*, *Cordia*, *Spathodea*. Insects such as Hymenoptera, Hemiptera, Homoptera and Coleoptera are caught in the air or picked from plant surface. Male establishes feeding territories in flowering trees.

Breeding. Nests found all year round but chiefly Jan-Mar (Guianas). Small cup-shaped nest built on horizontal branch in large tree, normally above 10 m. Clutch size 2; incubation 15 days, by female; chick black with sparse, dark grey dorsal down; fledging period 24-25 days; young remain with adult female for 3-4 weeks. First breeding in second year.

Movements. Sedentary along coastal areas; follows flowering seasons of trees inland.

Status and Conservation. Not globally threatened. CITES II. Locally common, particularly in mangrove swamps and marshy coastal areas; less numerous inland. Has become a rather rare resident on Trinidad due to the loss of mangrove and swamp since the early 1980's; present at Caroni Swamp. Regularly recorded at Cayenne and Mana (French Guiana).

Bibliography. Bangs & Penard (1918), Chubb (1916), French (1991), Grantsau (1988), Haverschmidt & Mees (1994), Herklots (1961), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Olrog (1968), Ruschi (1953a, 1981-1982, 1986), Sick (1993, 1997), Snyder (1966), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Street (1946), Tostain *et al.* (1992).

58. Green-breasted Mango

Anthracothorax prevostii

French: Mango de Prévost **German:** Grünbrust-Mangokolibri **Spanish:** Mango Pechiverde
Other common names: Green-breasted Hummingbird; Prévost's Mango (*prevostii*); Ecuadorian Mango (*iridescens*)

Taxonomy. *Trochilus prevostii* Lesson, 1832, Veracruz, Mexico.

Forms superspecies with *A. nigricollis* and *A. veraguensis*, and probably also *A. viridigula*. Very closely related to *A. nigricollis*, and occasionally regarded as conspecific, the two evidently replacing each other geographically, with at most very local sympatry in N Venezuela, SW Colombia and perhaps elsewhere. Often considered conspecific with *A. veraguensis*. Race *iridescens* has alternatively been treated as a race of *A. nigricollis*, or a full species. Proposed race *nigrilineatus* of Bay Is (Honduras) now held to be inseparable from *gracilirostris*; proposed *pinchoiti* of San Andrés I generally regarded as inseparable from *hendersoni*. Five subspecies currently recognized.

Subspecies and Distribution.

A. p. prevostii (Lesson, 1832) - E & S Mexico S to Guatemala, Belize and (possibly migrants) El Salvador.

A. p. gracilirostris Ridgway, 1910 - El Salvador and Honduras S to C Costa Rica.

A. p. hendersoni (Cory, 1887) - San Andrés I and Providencia I in W Caribbean.

A. p. viridicordatus Cory, 1913 - extreme NE Colombia (Guajira Peninsula) and coastal slope of N Venezuela.

A. p. iridescens (Gould, 1861) - arid upper Cauca Valley (W Colombia), and coastal slope of SW Ecuador and extreme NW Peru.



Descriptive notes. 11-12 cm; male 7.2 g, female 6.8 g (*gracilirostris*). Male bronzy-green above, bright green below, centre of throat and breast extensively black, bordered laterally with deep blue; outer four rectrices purple, narrowly edged with black. Female mostly white below with green sides and a broad central stripe of black mixed with green, outer four rectrices with subterminal black-band and narrow white tip; plumage of a small proportion of adult females like that of adult male and apparently requires two or more years to attain. Young bird has dark central stripe bordered or smudged with rufous (including *iridescens*, and unlike *A. nigricollis*) and buffy fringes over much of back. Race *gracilirostris* has shorter, more slender bill than nominate and upperparts less golden green; *viridicordatus* has upperparts grass green, undertail-coverts darker, central rectrices more olive-green; *hendersoni* is more bronzy-green above and black throat-stripe of male much less conspicuous; most distinct is *iridescens*, in which the black of the throat and chest of the male is much more extensive, approaching *A. nigricollis*, but female resembles that of *prevostii* in having central black stripe mixed with green and greater extent of white on lower face.

Habitat. Open grassy or shrubby areas with scattered taller trees, especially near water; savannas, pastures, parks, gardens, shaded coffee plantations, also borders of gallery woodland and mangroves, tall second growth. Mostly lowlands, locally to 900-1200 m.

Food and Feeding. Visits mostly flowers of trees (*Inga*, *Caesalpinia*, *Bauhinia*, *Erythrina*, *Ceiba*, *Calycophyllum*), vines and lianas (*Combretum*, *Ipomoea*) and shrubs (*Hibiscus*, *Quassia*), usually well above ground; several may gather at a large flowering tree where aggressive males sometimes defend feeding territories. Frequently flycatches high in the air, sallying from perch or during prolonged bouts of hovering and darting; also gleans arthropods from foliage, spiderwebs, or window screens.

Breeding. Mainly during dry season, Dec-May in Costa Rica, Oct and Feb-Mar in El Salvador, Mar in N Colombia. During breeding season male sings a buzzy, twangy song of short phrases rapidly repeated 3-4 times per bout, from song perches high in isolated trees, or in flight between perches. Nest a shallow cup of light-coloured plant down and cobweb, decorated sparsely or not at

all with bits of bark or lichen, situated on high outer twig of leafless or sparsely-foliaged tree, 15-25 m above ground. Clutch size 2. No further information.

Movements. Ranges rather widely following changes in flowering on a local basis, but no long-distance migration known. Nominate strays to extreme S USA.

Status and Conservation. Not globally threatened. CITES II. Uncommon to very common in different parts of range, and in many areas expanding range with deforestation; readily accepts man-made habitats, e.g. city parks and gardens with scattered fruit trees. Occurs in Santa Rosa and Palo Verde National Parks (Costa Rica); also regularly recorded at Tecolutla, Sierra de Los Tuxtlas, Tuxtpec, Yaxchilán and Uxmal (Mexico).

Bibliography. Bond (1950, 1985), Butler (1979), DeBenedictis (1994), Dickey & van Rossem (1938), Fogden (1993), Friedmann *et al.* (1950), Hilty & Brown (1986), Howell, S.N.G. & Webb (1995a), Howell, T.R. (1957), Johnsgard (1997), Land (1970), Lowery & Dalquest (1951), Meyer de Schauensee & Phelps (1978), Monroe (1968), Parker *et al.* (1982), Raffaele *et al.* (1998), Ridgely & Gwynne (1989), Ridgway (1911), Russell (1964), Russell *et al.* (1979), Slud (1964, 1980), Smith (1966), Stiles (1985c), Stiles & Skutch (1989), Stotz *et al.* (1996), Wagner (1946a), Warner & Mengel (1951), Wolf (1970), Zimmer (1950d).

59. Black-throated Mango

Anthracothorax nigricollis

French: Mango à cravate noire

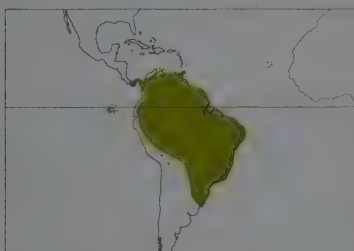
German: Schwarzbrust-Mangokolibri

Spanish: Mango Gorginegro

Taxonomy. *Trochilus nigricollis* Vieillot, 1817, Brazil.

Forms superspecies with *A. prevostii* and *A. veraguensis*, and probably also *A. viridigula*. Very closely related to *A. prevostii*, and occasionally regarded as conspecific, the two evidently replacing each other geographically, with at most very local sympatry in N Venezuela. SW Colombia and perhaps elsewhere; *A. p. iridescens* has alternatively been attributed to present species. Monotypic.

Distribution. W Panama and Colombia E to Trinidad and Tobago and the Guianas, and S to Peru, E Bolivia, Paraguay, NE Argentina and S Brazil.



Descriptive notes. 11-12 cm; male 6-9 g, female 7-3 g. Male has slightly decurved black bill; upperparts bronzy-green; underparts, centre of breast and abdomen velvet black bordered with iridescent blue-green; tail mainly deep chestnut, glossed purple, edged dark blue. Female bill similar to male; upperparts as male; on underparts, central stripe from chin to abdomen velvet black, broadly bordered white on both sides; tail as in male but with broad blackish subterminal band, tipped white. Immature like adult female with feathers on head and lower back edged brown.

Habitat. Open garden-like vegetation with bushes and scattered trees; cultivated slopes of mountain ranges. Normally confined to tropical areas up to 1000 m.

Food and Feeding. Nectar of mainly tall flowering trees (*Erythrina*, *Tabebuia*, *Spathodea*), also feeds at vines and shrubs (*Russelia*, *Ixora*, *Hibiscus*). Hawks for insects in the open, often high above tree tops or among foliage. Male occupies feeding territories in flowering trees.

Breeding. Dec-Jul. Small cup-shaped nest made of fine, whitish plant material decorated with lichen, usually saddled on horizontal branch and rather exposed, normally at 8-15 m, rarely lower. Clutch size 2; incubation period 16-18 days, by female; young blackish, 2 rows of greyish natal down; fledging period 20-24 days, young remaining with female for 3-4 weeks; 2 broods. First breeding in second year.

Movements. Migration to higher altitudes in Aug-Sept; long-distance migration reported from E Brazil.

Status and Conservation. Not globally threatened. CITES II. Common in cultivated areas; also commonly seen in parks of big cities, e.g. Asunción (Paraguay) and Caracas (Venezuela); one of the most easily seen hummingbirds in many areas. Densities on Trinidad (Arima Valley) at least 8-12 birds/km², in Colombia (Valle del Cauca) at least 6-8 birds/km².

Bibliography. Belton (1984), Bertonatti & Heinonen (1988), Berton (1930), Bond & Meyer de Schauensee (1943), Borrero (1972), Broom (1976), Canevari *et al.* (1991), Contreras (1992), Contreras *et al.* (1990), Cotton (1998a), Feinsinger (1980), ffrrench (1991), Fisher & Wetmore (1931), Fritsch & Schuchmann (1988), Grantsau (1988), Gyldestolpe (1945b), Hartman & Lessler (1963), Haverschmidt & Mees (1994), Hayes (1995), Hayes & Samad (1998), Hellmayr (1929), Herklotz (1961), Herrera (1998), Hilty & Brown (1986), Krüger *et al.* (1982), Labude (1986), Meyer de Schauensee & Phelps (1978), Munves (1975), Navas & Bo (1993), Olivares (1963), Olivares & Hernández (1962), Oniki (1996), de la Peña (1994), Pereyra (1950), Pople *et al.* (1997), Quesnel (1995), Ridgely & Gwynne (1989), do Rosário (1996), Ruschi (1957b, 1967d, 1973d, 1981-1982, 1982a, 1986), Rutgers & Norris (1972), Saibene *et al.* (1996), Schuchmann & Prinzing (1987), Short (1975), Sick (1993, 1997), Snow, B.K. & Snow (1972), Snow, D.W. & Snow (1980), Steinbacher (1962), Stotz *et al.* (1996), Street (1946), Tostain *et al.* (1992), Voous (1983), Wetmore (1939, 1968a), Willis & Eisenmann (1979), Zimmer (1950d).

60. Veraguas Mango

Anthracothorax veraguensis

French: Mango de Veragua

German: Veragua-Mangokolibri

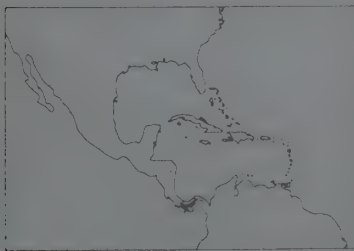
Spanish: Mango de Veragua

Taxonomy. *Anthracothorax veraguensis* Reichenbach, 1855, Veragua, Panama.

Forms superspecies with *A. prevostii* and *A. nigricollis*, and probably also *A. viridigula*. Often considered a race of *A. prevostii*. Monotypic.

Distribution. Panama, in Pacific lowlands from Chiriquí to S Cocle; two records from Caribbean side of Canal Zone (Gatún).

Descriptive notes. 11-12 cm; 7-0 g. Male has slightly decurved black bill; upperparts metallic bronzy-green; underparts shiny green, bluish on breast and centre of belly; tail mostly maroon, tipped black. Female bill similar to male; upperparts metallic green; underparts white from chin to lower abdomen with broad central stripe of greenish blue; tail blackish, outer rectrices tipped white. Immature like female, but with rufous-bordered central stripe.



Habitat. Open vegetation of pastures and stream edges with shrubs and scattered trees.

Food and Feeding. Nectar of flowering shrubs such as *Calliandra*, and trees such as *Erythrina* and *Inga*, from near ground to 10 m. Territorial at mass-flowering trees.

Breeding. No information.

Movements. Apparently sedentary, little information available.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in South Central American Pacific Slope EBA. Locally common. A poorly studied species; extensive research required.

Bibliography. Anon. (1998a), Olson (1993), Ridgely & Gwynne (1989), Wetmore (1968a).

61. Antillean Mango

Anthracothorax dominicus

French: Mango doré

German: Dominikanermangokolibri

Spanish: Mango Antillano

Other common names: Puerto Rican Golden Hummingbird

Taxonomy. *Trochilus dominicus* Linnaeus, 1766, Hispaniola.

Appears to be closely related to *A. mango*. Two subspecies recognized.

Subspecies and Distribution.

A. d. dominicus (Linnaeus, 1766) - Hispaniola and offshore islands of Tortue, Gonâve, Vache and Beata.

A. d. aurulentus (Audebert & Vieillot, 1801) - Puerto Rico and offshore islands of Culebra and Vieques, and Virgin Is (St Thomas, St John, Anegada).



Descriptive notes. 11-12.5 cm; male 6-8 g, female 4-7 g. Male has slightly curved black bill; upperparts shiny green-bronze; chin and throat metallic green, rest of underparts velvet black; tail violet with blue-black tips. Female bill similar to male's; upperparts shiny green-bronze; small white spot behind eye; underparts grey, pale white on abdomen. Immature similar to adult female with velvet black median line, no white spot behind eye. Male *aurulentus* smaller than nominate, with gorget brighter, less black below; female with outer tail feathers basally brownish grey, not violaceous chestnut as in nominate.

Habitat. Clearings, gardens, secondary growth and arid shrubby hillsides along the coast, rare above 800 m and inside forests.

Food and Feeding. Nectar of flowering *Cordia*, *Melocactus*, *Bauhinia*, *Ipomea*, *Hibiscus*, *Erythrina*, *Sabineia*, etc. Insects are caught in the air, spiders collected from the surface of leaves and bark. Forages from lower mid-strata to tree tops. Male defends nectar-rich territories.

Breeding. Mar-Nov. Compact cup-shaped nest, lined with soft plant fibre, often coated with lichen, built mainly in tree at 3-12 m. Clutch size 2; chick black with two rows of greyish dorsal down; single brood. No further information available.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Hispaniola EBA and Puerto Rico and the Virgin Islands EBA. Generally common in coastal areas with scattered trees. Probably extinct now on St John and Anegada (Virgin Is) and perhaps also on Vieques, while rare on E Puerto Rico, apparently all as a result of competition from *Eulampis holosericeus*.

Bibliography. Anon. (1998a), Biaggi (1983), Bond (1985), Dod (1987, 1992), Kodric-Brown *et al.* (1984), Otero (1998), Raffaele (1989), Raffaele *et al.* (1998), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Tyrrell & Tyrrell (1990), Wetmore (1927), Wetmore & Swales (1931).

62. Green Mango

Anthracothorax viridis

French: Mango vert

German: Smaragd mangokolibri

Spanish: Mango Portorriqueño

Other common names: Puerto Rican Mango

Taxonomy. *Trochilus viridis* Audebert and Vieillot, 1801, Puerto Rico.

Monotypic.

Distribution. Puerto Rico.



Descriptive notes. 11-14 cm; 7 g. Sexes alike. Bill slightly curved, black; upperparts emerald green; underparts metallic blue-green; tail metallic blue-black, rounded. Adult female with tiny white eye-spot, lacking in male. Immature with brownish-tinged feathers on head and back.

Habitat. Plantations and forests of C and W mountains. Rare in coastal areas. Most common between 800 and 1200 m.

Food and Feeding. Nectar of flowering trees, shrubs and vines, such as *Pariti tilaceum*, *Leonotis leonotum*, *Quisqualis indica* and *Ipomea* sp. Insects are caught in the air, often above tree tops. Spiders collected from the surface of leaves are another important protein source.

Indigestible chitinous food remains are regurgitated as pellets. Forages from low understorey to tree-top levels. Male defends territories at flowering trees.

Breeding. Nest records Oct-May. The nest is a soft, compact cup decorated externally with lichen; attached to vertical branch of high tree, normally above 8 m. Clutch size 2; chick black with 2 rows of dorsal down; single brood. No further information available.

Movements. Altitudinal movements depending on flowering seasons.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Puerto Rico and the Virgin Islands EBA. Common resident in the C and W mountains of Puerto Rico. Readily accepts man-made habitats like coffee plantations.

Bibliography. Anon. (1998a), Biaggi (1983), Bond (1985), Kodric-Brown *et al.* (1984), Ornelas (1994), Raffaele (1989), Raffaele *et al.* (1998), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Tyrrell & Tyrrell (1990), Wetmore (1927).

63. Jamaican Mango

Anthracothorax mango

French: Mango de la Jamaïque **German:** Jamaikamangokolibri **Spanish:** Mango Jamaicano
Other common names: Black Mango

Taxonomy. *Trochilus Mango* Linnaeus, 1758, Jamaica.

Appears to be closely related to *A. dominicus*; closest Central American relative is probably *A. prevostii*. Monotypic.

Distribution. Jamaica.



Descriptive notes. 11-12 cm; 8-5 g. Medium-sized darkish hummingbird easily distinguishable from all other *Anthracothorax* species. Male has bill slightly curved, black; crown faded green, sides of head and neck metallic magenta purple; below velvet black, back dull green-bronze; central tail feathers dusky bronze to dull black, rest metallic violet with narrow dark blue band. Female similar to male; faded green velvet on flanks; outer tail feathers tipped white. Immature male with deep blue throat becoming velvety after the second year.

Habitat. Wide range of open and semi-open lowland vegetation including arid areas, gardens and plantations. Common along forest edges from sea-level to 800 m. Regular but rare, except for Jun-Aug., at natural edges of wet mid-altitude and elfin forest at 900-1500 m; scarce in mangroves.

Food and Feeding. Nectar from a wide variety of bird-adapted flowers of indigenous and introduced plants: *Hohenbergia*, *Opuntia*, *Stenocereus*, *Cordia*, *Tabebuia*, *Spathodea*, *Bauhinia*. Males are territorial at mass-flowering trees. Small arthropods caught on the wing in open space, often at 10-15 m.

Breeding. Nests all year round, most frequently during Jan-May. Small cup-shaped nest of densely woven silky fibres and cobwebs saddled on thick branch of tree at 3-8 m. Clutch size 2; incubation by female; chick blackish, 2 rows of greyish dorsal down; single brood. No further information.

Movements. Birds disperse to mid-altitude regions (Cockpit Country) and to Blue and John Crow Mts in Jun-Aug, following the flowering season at higher altitudes.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Jamaica EBA. Common resident. Particularly common along northern coastal areas with densities of at least 5-8 individuals/km². Ready occupation of man-made habitats suggests that habitat loss is unlikely to be a problem.

Bibliography. Anon. (1998a), Bond (1985), Danforth (1928), Downer & Sutton (1990), Lack (1976), Pearson (1980), Raffaele *et al.* (1998), Salmon (1972), Stattersfield *et al.* (1998), Stoltz *et al.* (1996), Schuchmann (1980a, 1980b, 1980c, 1990a), Tyrrell & Tyrrell (1990).

64. Fiery-tailed Aowlbill

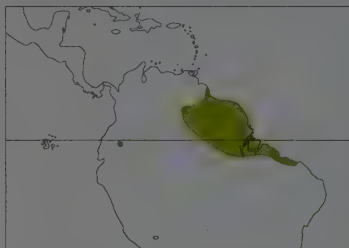
Anthracothorax recurvirostris

French: Colibri avocette **German:** Schwarzbauch-Avosettkolibri **Spanish:** Mango Picolezn
Other common names: Swainson's Hummingbird, Fiery-tailed Avocetbill

Taxonomy. *Trochilus recurvirostris* Swainson, 1822, Peru; error = Cayenne.

Normally placed in monospecific genus *Avocettula*, mainly due to remarkable form of bill; other details of morphology, however, together with behaviour and nest structure, support positioning within *Anthracothorax*. Monotypic.

Distribution. SE Venezuela (Bolívar) and the Guianas to NC Brazil (lower Amazon E to Maranhão and Piauí); E Ecuador (Napo Valley).



Descriptive notes. 8-10 cm; 4-3 g. Male has short bill, strongly upturned at tip, black; back green; throat and breast glittering emerald, centre of belly black, sides dull green; tail violet above, central feathers green. Female similar to male, underparts white with central black stripe, sides copper-green; tail shows more blue-black, and outer feathers tipped white. Immature like adult female with tail coppery red underneath.

Habitat. Occurs in open savanna-like vegetation near granite outcrops within primary forest from sea-level to 500 m, occasionally at edges of low secondary vegetation near rivers.

Most numerous around 100-200 m. Foraging height around 1-3 m.

Food and Feeding. Collects nectar at the periphery of flowering *Clusia* and *Dioclea* shrubs. Hawks for insects in the air or gleans them from the underside of leaves. Feeds mainly by trap-lining.

Breeding. Sept-Dec in Surinam, records from Jul for French Guiana and N Brazil. Cup-shaped nest very small, saddled on thick horizontal branch of tall shrub or tree at 5-12 m. Clutch size 2; incubation by female; young black with sparse whitish dorsal down. No further information available.

Movements. Presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Currently considered Near-threatened. Widespread but generally considered rare; restricted to small areas of suitable habitat, particularly inselbergs. In the Voltzberg area of Surinam density of at least 2 individuals/km² recorded.

Bibliography. Bené (1947), Berlepsch (1908), Best *et al.* (1997), Butler (1979), Grantsau (1988), Haverschmidt & Mees (1994), Ingels (1981), Meyer de Schauensee & Phelps (1978), Ruschi (1981-1982, 1986), Schuchmann-Wegert & Schuchmann (1984), Sick (1993, 1997), Snyder (1966), Stoltz, Fitzpatrick *et al.* (1996), Stoltz, Lanyon *et al.* (1997), Tostain *et al.* (1992), Trail (1978).



PLATE 50

inches 2
cm 5

Genus *TOPAZA* G. R. Gray, 1840

65. Crimson Topaz

Topaza pella

French: Colibri topaze **German:** Rotnacken-Topaskolibri **Spanish:** Colibrí Topacio
Other common names: Topaz/Topaz-throated/King Hummingbird, Beautiful Topaz; Fiery/Inca Topaz (*pyra*)

Taxonomy. *Trochilus Pella* Linnaeus, 1758, Surinam.
Genus probably related to *Eulampis* and *Anthracothorax*, on basis of form of nest and display; has traditionally been placed close to *Oreotrochilus*. Race *pyra* often considered a separate species, but size and colour patterns indicate geographical variation only at subspecies level; some individuals of nominate race show glittering orange belly, thus resembling *pyra*. Race *smaregdula* has been proposed for birds of French Guiana, but not separable from nominate. Four subspecies currently recognized.

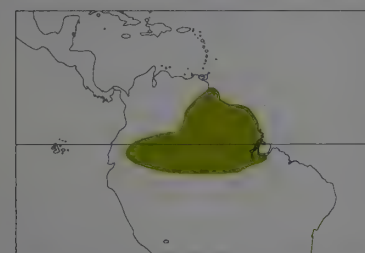
Subspecies and Distribution.

T. p. pyra (Gould, 1846) - SE Colombia, E Ecuador and NE Peru to NW Brazil (R Negro) and S Venezuela (Amazonas).

T. p. pamprepta Oberholser, 1902 - E Ecuador (Suno, R Napo).

T. p. pella (Linnaeus, 1758) - S Venezuela (E Bolívar) and the Guianas to N Brazil (Amapá).

T. p. microrhyncha Butler, 1926 - NC Brazil, along S bank of lower Amazon in vicinity of Belém.



Descriptive notes. Male 21-23 cm (including bill 4.3 cm and tail 12-13 cm), 10-14 g; female 13-14 cm, 10 g. A large, strikingly coloured species. Male has straight black bill; top and sides of head and neck velvet black; back glittering crimson to purple, golden on uppertail-coverts; throat bright green with a golden sheen, surrounded by a black band, underparts bright red, undertail-coverts bronze; wings brown; central tail feathers bronzy golden-green, outer tail feathers chestnut, submedian tail feathers elongated and crossed. Female bill similar to male's; back dark green; throat green with crimson discs, underparts green with

golden green discs, undertail-coverts shining green; central tail feathers bronzy, next pair violet, outermost pair chestnut. Immature like female. Male of *pyra* is glittering orange-red on underparts; tail bronze-green in centre, remainder blackish violet; female similar to nominate *pella* but tail blackish violet, only outer tail feathers with cinnamon outer web. Race *pamprepta* differs in shorter wing and longer tail; *microrhyncha*, the smallest of all races, with smaller bill, tends to have more reddish tone on throat patch, though this appears to vary clineally. Melanistic and albinotic individuals of the nominate race are relatively common.

Habitat. Occurs in lowland rainforests up to 500 m, mainly inland. Frequently found in tree tops of forests around granite outcrops and along gallery forests near river banks and creeks.

Food and Feeding. Mainly seen foraging for nectar in the upper storey of flowering forest trees such as *Inga* and *Bombax*, but also visits flowers of vines and epiphytes, e.g. Bromeliaceae, Gesneriaceae, Ericaceae. Occasionally found in much lower vegetation around inselbergs in Surinam where it forages for nectar near the ground at flowering stands of *Costus scaber* and in clumps of blooming *Pitcairnia nuda*. Male establishes feeding territories. Insects are caught in the air, often high above tree tops.

Breeding. Jan-Apr and again in Jul-Nov in the Guianas; no nesting data from other areas. Nests found at 3-8 m, often on vertical branches or in vines above or near water. The cup-shaped nest, consisting of soft greyish or brownish fibres of *Bombax* seeds and cobweb, is fairly small compared with the size of the bird. Clutch size 2; incubation by female, time unknown; chick black with some pale grey dorsal down; fledging period 21 days; young remain with female for 3 weeks. First breeding in the second year.

Movements. Mainly sedentary during the reproductive periods, thereafter number of individuals may decrease locally, probably following flowering season elsewhere.

Status and Conservation. Not globally threatened. CITES II. Locally common but frequently considered rare due to its secretive habits in the tree tops. In Guyana (Demerara River) more than 10 individuals/km² have been reported, and at least 8-12 individuals/km² near Voltzberg Nature Reserve in Surinam. No abundance data available for Amazonia and the western range of the species. Appears to have declined following extensive logging in E Ecuador (R Napo); race *pamprepta* has not been recorded in the Río Napo area for decades. Present in Imataca Forest Reserve (Venezuela), also (*pyra*) in Cuyabeno National Park (Ecuador).

Bibliography. Berlioz (1964), Blake (1950b), Butler (1979), Davis (1958), Grantsau (1988), Haverschmidt & Mees (1994), Hilty & Brown (1986), Ingels (1981), Meyer de Schauensee & Phelps (1978), Nicholson (1931), Norton (1965), Parker *et al.* (1982), Penard & Penard (1910), Peres & Whittaker (1991), Ruschi (1973d, 1977, 1981-1982, 1982a, 1986), Rutgers & Norris (1972), Schuchmann (1982a), Sick (1993, 1997), Snyder (1966), Stotz, Fitzpatrick *et al.* (1996), Stotz, Lanyon *et al.* (1997), Tostain *et al.* (1992), Willard *et al.* (1991), Zimmer (1951a).

Genus *EULAMPIS* Boie, 1831

66. Purple-throated Carib

Eulampis jugularis

French: Colibri madère **German:** Purpurkehlkolibri **Spanish:** Colibrí Caribeño Gorgimorado
Other common names: Purple/Purple-breasted Carib, Garnet/Red-breasted Hummingbird

Taxonomy. *Trochilus jugularis* Linnaeus, 1766, Cayenne and Surinam; error = Lesser Antilles.

Genus closely related to *Anthracothorax* and *Topaza*. Monotypic.

Distribution. Lesser Antilles, from Saba, St Eustatius, St Kitts, Nevis, Antigua and Montserrat through Guadeloupe, Dominica and Martinique to St Lucia and St Vincent.



Descriptive notes. 11-12 cm; male 9-12 g, female 7-10 g. Male has short bill, slightly curved, black. A sturdy, dark velvet hummingbird. Malar region, throat and chest fiery purplish red; undertail and uppertail-coverts metallic greenish blue; wings bright golden green. Female similar to male but bill longer and more decurved. Immature throat and chest orange with red speckles.

Habitat. Forest edges and tree tops of secondary and primary forest at altitudes of 800-1200 m.

Food and Feeding. Nectar of indigenous (*Cordia*, *Clusia*) and introduced trees (*Spathodea*, *Delonix*, *Caesalpinia*). Forages from mid-

strata to tree tops; occasionally visits flowering stands of *Heliconia caribaea* and banana (*Musa*) at heights of 2-3 m. Hawks for small insects on the wing, more frequently seen gleaning arthropods from leaves and spider webs. Male holds flower-centred territories all year round, female only during non-breeding season.

Breeding. Feb-May, occasionally Jan-Sept. Cup-shaped compact nest on vertical branch in tree at 3-5 m, rather small compared with the size of the bird. Nest material consists of soft plant fibres and spider web, occasionally camouflaged with thin strips of bark, moss or lichen on the outer nest wall. Clutch size 2; incubation 17-19 days, by female; chick darkish, two dorsal rows of down; fledging period 17-20 days; young remain with female for 2-3 weeks; single brood. Female very territorial around the nest, attacking even much larger species within 10 m of the nest.

Movements. On some islands (St Lucia, St Vincent) individuals occur at sea-level at end of May. Casual occurrence on Barbuda, Désirade, Is des Saintes and Bequia (Grenadines); sight records for Grenada and Barbados; rare straggler to the Greater Antilles.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Lesser Antilles EBA. Common resident in forests and plantations at higher altitudes. Density in the Edmond Forest Reserve on St Lucia at least 8-12 pairs/km². Ready occupation of man-made habitats suggests that habitat loss is unlikely to be a problem.

Bibliography. Anon. (1998a), Belton (1996), Bond (1985), Chávez-Ramírez & Dowd (1992), Chávez-Ramírez & Tan (1993), Hainsworth & Wolf (1970), Ingels (1976a, 1976b), Keith (1997), Krüger *et al.* (1982), Kunze (1984), Lack (1973), Leck (1973), Lodge (1896), Mobbs (1976), Norton & Hobbs (1987), Raffaele *et al.* (1998), Rutgers & Norris (1972), Schuchmann (1977b, 1978a, 1979f, 1980c, 1981), Schuchmann & Jakob (1981b), Schuchmann & Prininger (1987), Schuchmann & Schuchmann-Wegert (1984), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Tyrrell & Tyrrell (1990), Wolf (1975b, 1975c), Wolf & Wolf (1971), Zusi & Bentz (1984).

67. Green-throated Carib

Eulampis holosericeus

French: Colibri falle-vert **German:** Blaustern-Antillenkolibri **Spanish:** Colibrí Caribeño Gorgiverde
Other common names: Emerald-throated Carib/Hummingbird, Green Doctor Bird, Green Carib

Taxonomy. *Trochilus holosericeus* Linnaeus, 1758, Lesser Antilles.

Genus closely related to continental *Anthracothorax* and *Topaza*. Sometimes placed in monotypic genus *Sericotes*, on basis of more naked tarsi, rounded tail, and different coloration. Two subspecies recognized.

Subspecies and Distribution.

E. h. holosericeus (Linnaeus, 1758) - E Puerto Rico and Lesser Antilles (except Grenada).

E. h. chlorolaemus (Gould, 1857) - Grenada.



Descriptive notes. 11-12.5 cm; male 5.6-7.8 g, female 5.5-5.5 g. Male has medium-sized bill, slightly decurved, black. Upperparts metallic bronzy-green, uppertail-coverts blue-green; malar region, chin and throat metallic green, breast centre violet-blue, belly velvet black, undertail-coverts metallic blue; tail dark blue, rounded. Female similar to male, bill longer and more decurved. Immature like female, head feathers tinged brown. Race *chlorolaemus* differs from nominate by darker green throat and broad deep violet-blue patch on centre of breast.

Habitat. Open secondary vegetation, cultivated

areas, parks, semi-deciduous and rainforest at all elevations. More common from sea-level to 500 m.

Food and Feeding. Nectar of flowers of shrubs and small trees 1-4 m in height. Occasionally territorial at *Lantana* and *Bryophyllum* bushes. Forages for insects in the air, collects small spiders from webs.

Breeding. Feb-May. Compact cup-shaped nest is built at 1-4 m on the periphery of trees and bushes. Nest is placed in a saddle-like position on twigs, camouflaged outside by pieces of bark and lichen. Nest inside lined with soft fibres of seeds, cacti and tree ferns. Clutch size 2; incubation 17-19 days, by female; chick flesh-coloured, dorsally two rows of down; fledging period 20-22 days; young remain with female for 3-4 weeks; normally one brood. First breeding in second year.

Movements. Individuals disperse in Jun-Sept to forest borders at higher altitudes at c. 800-1000 m.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Puerto Rico and the Virgin Islands EBA and Lesser Antilles EBA. Common resident. Particularly numerous at sea-level on Basse Terre, Guadeloupe, with densities of at least 5-7 pairs/km². Ready occupation of man-made habitats suggests that habitat loss should pose no danger.

Bibliography. Anon. (1998a), Bond (1985), Bos (1989), Chávez-Ramírez & Dowd (1992), Chávez-Ramírez & Tan (1993), Ingels (1976a), Keith (1997), Lack (1973), Leck (1973), Moller (1930), Raffaele (1989), Raffaele *et al.* (1998), Rutgers & Norris (1972), Schuchmann (1979b, 1980c, 1981), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Tyrrell & Tyrrell (1990), Wolf (1975c).

Genus *CHRY SOLAMPIS* Boie, 1831

68. Ruby Topaz

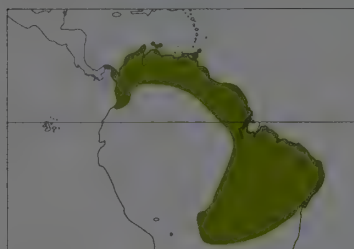
Chrysolampis mosquitus

French: Colibri rubis-topaze

German: Moskitokolibri

Spanish: Colibrí Rubí

Other common names: Ruby-topaz Hummingbird

Taxonomy. *Trochilus Mosquitus* Linnaeus, 1758, Surinam.Closely related to *Orthorhynchus*, and may even be congeneric. Monotypic.**Distribution.** E Panama and W, N & C Colombia E through Venezuela to the Guianas, then S through NE & C Brazil (Pará to Pernambuco and S to Mato Grosso) to E Bolivia; also islands along N coast from Aruba, Curaçao and Bonaire E to Trinidad and Tobago.**Descriptive notes.** 8-9 cm; 4-5 g. Male has short straight black bill; crown and nape shining ruby red (occasionally orange), back dark brown glossed dull olive; throat and breast iridescent golden (occasionally emerald-green); rest of underparts brown; tail rich chestnut tipped black. Female has copper-green back; below pale grey (on both Trinidad and Tobago, some birds have greenish-golden stripe from chin to breast); central tail feathers olive-green, the others rufous-chestnut with shining purple-black subterminal band, tipped white. Immature similar to adult female; has white spot behind eye,

outer tail dark violet, tipped white.

Habitat. Occurs in savanna-like vegetation from sea-level to shrubby arid hillsides at 1700 m; forages from low down to treetops in clearings, open country, gardens and cultivated areas. Most numerous below 500 m; birds at higher altitudes are currently not breeding.**Food and Feeding.** Nectar of flowering shrubs, cultivated crops, cacti, small and large trees: *Russelia*, *Cajanus*, *Iseria*, *Melocactus*, *Citharexylum*, *Samanea*, *Cordia*. Small insects are caught in the air by hawking. Occasionally seen foraging for arthropods among foliage along clearings and roads. Male defends feeding territories in flowering shrubs or trees.**Breeding.** Dec-Jun on Trinidad and Tobago, Venezuela, Guianas; Sept-Jan in Brazil. Tiny cup-shaped nest of fine plant fibre and cobweb, outside decorated with lichen and/or pieces of bark, is built in fork of small branch, 1-4 m above ground, occasionally up to 8 m. Clutch size 2; incubation 15-16 days, by female; chick black with sparse brownish dorsal down; fledging in 19-22 days. First breeding in second year.**Movements.** Migratory. Arrives in the southern Cauca Valley, Colombia, in May and disappears in Sept; absent or rare on Trinidad and Tobago in Aug-Nov; appears in Paraná, Brazil, in Oct and leaves in Apr. Within Brazil, N-S migration; along the coastal areas of the Guianas, Venezuela and Colombia presumably an E-W migration with southward tendency towards Cauca and Magdalena Valleys, Colombia.**Status and Conservation.** Not globally threatened. CITES II. Common resident in the lowlands and coastal ranges, with densities of at least 6-8 pairs/km² in shrub-like habitats of SW Trinidad. Readily accepts man-made habitats like gardens and cultivated areas. Present in Tayrona National Park (Colombia). Until 1970 the most sought-after species of hummingbird for the international bird trade in Brazil; this has now been ended.**Bibliography.** Allen (1961), Bos (1989), Braun & Wolf (1987), Craigie (1928), Feinsinger (1980), French (1991), Friedmann & Smith (1950), Grantsau (1988), Haverschmidt & Mees (1994), Herklots (1961), Hilty & Brown (1986), Meyer de Schauensee & Phelps (1978), Mobbs (1969, 1977), Oniki (1996), Raw (1996), Remsen & Traylor (1989), Ridgely & Gwynne (1989), do Rosário (1996), Ruschi (1953b, 1962f, 1964d, 1967a, 1973d, 1981-1982, 1982a, 1986), Rutgers & Norris (1972), Salaman & Mazariegos (1998a), Sanft (1970), Schürer (1983), Sick (1993, 1997), Snow & Snow (1972), Snyder (1966), Stotz *et al.* (1996), Tostain *et al.* (1992), Voous (1983).Genus *ORTHORHYNCUS* Lacépède, 1799

69. Antillean Crested Hummingbird

Orthorhynchus cristatus

French: Colibri huppé

German: Antillenhaubenkolibri

Spanish: Colibrí Crestado

Other common names: Crested Hummingbird

Taxonomy. *Trochilus cristatus* Linnaeus, 1758, Barbados.Closely related to *Chrysolampis*, and may even be congeneric. Four subspecies recognized.**Subspecies and Distribution.***O. c. exilis* (J. F. Gmelin, 1788) - E Puerto Rico S through Lesser Antilles to St Lucia.*O. c. ornatus* Gould, 1861 - St Vincent.*O. c. cristatus* (Linnaeus, 1758) - Barbados.*O. c. emigrans* Lawrence, 1877 - Grenadines and Grenada.**Descriptive notes.** 8-9.5 cm; male 4 g, female 3-5 g. Male has short straight black bill; head with green crest, tipped metallic green to bright blue-green, upperparts dull metallic bronze-green; underparts sooty black; tail black, rounded. Female bill similar to male's; head without crest, forehead, crown and upperparts metallic bronzy-green; underparts light grey; tail blackish, rounded, four outer rectrices broadly tipped whitish grey. Immature like female, head feathers tinged cinnamon. Races distinguished by crest colour: *exilis* wholly green or slightly tinged blue on tip; *ornatus* terminal portion abruptly blue; *cristatus* golden to emerald, violet terminally; *emigrans* like nominate but more bluish violet, throat paler grey; degree of paleness in underparts of female varies with race.**Habitat.** Open vegetation, parks, plantations, forest borders from sea-level to high mountains. Commonest below 500 m.**Food and Feeding.** Nectar of flowering shrubs (*Lantana*, *Euphorbia*), vines and from lower parts of hedges and trees (*Hibiscus*, *Bauhinia*, *Tabebuia*, *Delonix*). Small arthropods are collected from plant surfaces or hawked for in air.**Breeding.** Breeds all year round, chiefly Mar-Jun. Nest cup-shaped, build on thin branch of shrub or vine 1-3 m above ground, often shaded by leaves. Nest interior lined with soft plant fibre, outside decorated with pieces of dead leaves, lichens or bark. Clutch size 2; incubation 17-19 days, by female; chick darkish grey, two dorsal rows of down; fledging

period 19-21 days; young remain with female for 3-4 weeks; single brood. First breeding in second year.

Movements. Sedentary, with possible dispersal to higher altitudes in Jul/Aug. Race *exilis* is rare straggler to Florida, USA.**Status and Conservation.** Not globally threatened. CITES II. Restricted-range species: present in Puerto Rico and the Virgin Islands EBA and Lesser Antilles EBA. Common resident. Particularly common at sea-level, with densities of at least 6-10 pairs/km² on St Lucia, at least 4-8 pairs/km² on Guadeloupe, and at least 3-5 pairs/km² on Dominica. Widespread throughout Lesser Antilles, occurring at all altitudes and in all habitat types; ready occupation of man-made habitats suggests that habitat loss is unlikely to be a problem.**Bibliography.** Anon. (1998a), Biaggi (1983), Bond (1985), Bos (1989), Chávez-Ramírez & Tan (1993), DeBenedictis (1992), English (1928, 1934), Ingels (1976a, 1976b), Keith (1997), Krüger *et al.* (1982), Lack (1973), Leck (1973), Oberholser (1905), Pulich (1968), Raffaele (1989), Raffaele *et al.* (1998), Riley (1904), Rutgers & Norris (1972), Schuchmann (1979b, 1980c, 1981), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Tyrrell & Tyrrell (1990), Wolf (1975c).Genus *KLAIS* Reichenbach, 1854

70. Violet-headed Hummingbird

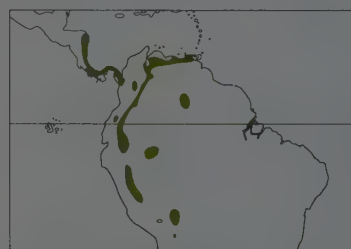
Klais guimeti

French: Colibri à tête violette

German: Violettekopfkolibri

Spanish: Colibrí Cabeciazul

Other common names: Violet-crowned Hummingbird(!)

Taxonomy. *Trochilus Guimeti* Bourcier, 1843, Caracas, Venezuela.Genus sometimes merged into *Abeillia*; closely related to *Stephanoxis*. Nominate and race *pallidiventr* intergrade in SE Ecuador. Three subspecies recognized.**Subspecies and Distribution.***K. g. merrittii* (Lawrence, 1860) - E Honduras to E Panama.*K. g. guimeti* (Bourcier, 1843) - N & W Venezuela through E Colombia and Ecuador to extreme N & NE Peru and extreme NW & N Brazil.*K. g. pallidiventr* Stolzmann, 1926 - E Peru and WC Bolivia.**Descriptive notes.** 7.5-8.5 cm; male 2-9 g, female 2-7 g. Bill of female averages slightly longer, but male has significantly longer wings and tail; bill black. Bronzy-green above, pale grey below; entire head (male) or crown (female) violet-blue; square white postocular spot more prominent than in other small hummingbirds; lateral rectrices black, subterminally tipped with dull white, more broadly in female. Young bird resembles adult female but with little or no blue or violet on crown. Racial variation is relatively slight: both sexes of race *merrittii* have crown distinctly bluish rather than violet; underparts of *pallidiventr* are

paler than those of other races.

Habitat. Canopy and edge of tall humid forest, tall second growth, tree plantations, shaded gardens and hedgerows in foothills and adjacent lowlands; mostly below 600 m (Honduras); 50-1200 m (Costa Rica); 400-1800 m (Colombia), 150-1900 m (Venezuela).**Food and Feeding.** Visits mostly small flowers of a variety of trees (*Inga*, *Warscewiczia*, *Hamelia*, *Hampea*, *Vismia*), shrubs (*Cephaelis*, *Psychotria*, *Besleria*, *Sabicea*, *Stachytarpheta*) and epiphytes (*Columnnea*, *Cavendishia*, bromeliads); male often territorial at flowers outside breeding season when not supplanted by larger, more aggressive species. Sallies from perch to catch flies and gnats, gleans foliage for arthropods, especially along edges and streams.**Breeding.** Mainly during dry season, Jan-May in Costa Rica. During breeding season males typically in leks of up to 10 but occasionally solitary. Nest a tiny, thick-walled cup of green moss and cobwebs, lined with soft plant down, typically on pendent twig or vine overhanging shaded stream, less often in forest understorey far from water, 1-5 m above ground. Clutch size 2; incubation at least 16 days. No further information.**Movements.** Basically sedentary, but performs some local movements in response to changing flower availability.**Status and Conservation.** Not globally threatened. CITES II. Common in many areas in Central America, such as La Selva Biological Station and Rara Avis reserve in Costa Rica; fairly common to uncommon in E Honduras; rare and possibly local in Colombia. Present in Corcovado and Braulio Carrillo National Parks and Golfito National Wildlife Refuge (Costa Rica), Los Katios National Park (Colombia) and Guatopo National Park (Venezuela).**Bibliography.** Bond & Meyer de Schauensee (1943), Butler (1979), Fogden (1993), Grantsau (1988), Hilty & Brown (1986), Howell, S.N.G. & Webb (1995a), Howell, T.R. (1957), Meyer de Schauensee & Phelps (1978), Monroe (1968), Moore (1950a), Parker *et al.* (1982), Remsen & Traylor (1989), Ridgely & Gwynne (1989), Ridgway (1911), Ruschi (1968, 1981-1982, 1986), Salaman & Mazariegos (1998b), Sick (1993, 1997), Skutch (1958), Slud (1964), Stiles (1980, 1985b), Stiles & Skutch (1989), Stone (1996), Stotz *et al.* (1996), Wetmore (1939, 1968a), Williams & Tobias (1994), Zimmer (1950d).

Genus *STEPHANOXIS* Simon, 1897

71. Plovercrest

Stephanoxis lalandi

French: Colibri de Delalande **German:** Spitzhaubenelfe **Spanish:** Colibrí Copetón
Other common names: Black-breasted/DeLalande's Plovercrest (*lalandi*); Violet-crested/Loddiges's Plovercrest (*loddigesii*)

Taxonomy. *Trochilus Lalandi* Vieillot, 1818, Brazil.

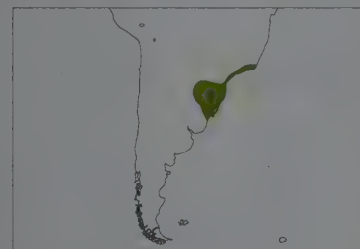
Genus closely related to *Klais*. Race *loddigesii* sometimes considered a distinct species, on basis of marked plumage differences. Species name has on occasion been erroneously emended to "*delalandei*". Two subspecies recognized.

Subspecies and Distribution.

S. l. lalandi (Vieillot, 1818) - E Brazil (S Minas Gerais, Espírito Santo, Rio de Janeiro, NE São Paulo).

S. l. loddigesii (Gould, 1831) - E Paraguay and NE Argentina (Misiones) to S Brazil (S São Paulo, Paraná, Santa Catarina, Rio Grande do Sul).

Descriptive notes. 8.5-9 cm; male 3.4 g, female 2.2 g. Male has bill straight, black; head with long iridescent green crest, occasionally crest bluish green, longest crest feather purplish black; sides of head grey, white spot behind the eye; upperparts shining bronze-green; chin to upper belly violet-blue, rest of underparts grey; central tail feathers green, outer ones green with subterminal blackish band, tipped greyish white. Female shining green above, grey below; head feathers slightly elongated. Immature like female. Race *loddigesii* has bill slightly longer; male differs from nominate by blue crest and more reduced, darker patch on



underparts: female similar to that of nominate.

Habitat. Understorey of forest, scrub vegetation and along water courses from sea-level to 900 m, occasionally seen at much higher altitudes (Serra do Caparão, Espírito Santo, 2900 m).

Food and Feeding. Forages for nectar at native and introduced flowers (*Vochysia*, *Salvia*, *Dombeya*, *Calliandra*, *Inga*, *Eucalyptus*), from near the ground to tree tops. Insects are caught in the air, also gleaned from leaves. Male establishes feeding territories mainly during reproductive period.

Breeding. Oct-Mar. Males gather at leks during the reproductive period. Cup-shaped nest of soft plant or seed fibres and cobweb is placed on forked branch in sheltered shrub or bamboo at 1-3 m. Clutch size 2; incubation 14-16 days, by female; chick has pale grey dorsal down; fledging at 24-28 days; young remain with adult for 3 weeks; one brood per year. First breeding in second year.

Movements. Largely sedentary, but in the south of breeding range individuals winter at lower elevation.

Status and Conservation. Not globally threatened. CITES II. Patchily distributed and only locally common, e.g. around Pôrto Alegre in Rio Grande do Sul (S Brazil). In C & S Paraná (along R Tibagi) densities of at least 3-5 pairs/km² noted in breeding season. Readily takes to man-made habitats such as farmland with scattered bushes and forest islands. Present in Serra dos Órgãos and Itatiaia National Parks (Brazil) and Estancia Itabo Private National Park and Mbaracayú Reserve (Paraguay).

Bibliography. Belton (1984), Berry (1989), Brooks *et al.* (1993), Canevari *et al.* (1991), Contreras *et al.* (1992), Forrester (1993), Grantsau (1988), Hayes (1995), Lowen, Bartrina, Clay & Tobias (1996), Lowen, Clay *et al.* (1995), Narosky & Yzurieta (1993), Navas & Bo (1993), Oniki (1996), Parker & Goerck (1997), de la Peña (1994), Pereyra (1950), do Rosário (1996), Ruschi (1973d, 1981-1982, 1982a, 1986), Rutgers & Norris (1972), Saibene *et al.* (1996), Sazima, I. *et al.* (1996), Sazima, M. *et al.* (1994), Scott & Brooke (1985), Sick (1993, 1997), Stotz *et al.* (1996), Tobias *et al.* (1993), Willis (1992).

Genus *ABEILLIA* Bonaparte, 1850

72. Emerald-chinned Hummingbird

Abeillia abeillei

French: Colibrí d'Abeillé **German:** Smaragdkehlkolibri **Spanish:** Colibrí de Abeillé
Other common names: Abeille's Hummingbird

Taxonomy. *Ornismya Abeillei* Lesson and DeLattre, 1839, Veracruz, Mexico.

Genus sometimes considered to incorporate *Klais*. Validity of race *aurea* has been questioned. Two subspecies recognized.

Subspecies and Distribution.

A. a. abeillei (Lesson & DeLattre, 1839) - SE Mexico to Guatemala, El Salvador and N Honduras.
A. a. aurea A. H. Miller & Griscom, 1925 - S Honduras and N Nicaragua.

Descriptive notes. 7-7.5 cm; 2.7 g. Male has short straight black bill; back metallic bronze-green; broad white postocular spot; chin and upper throat shining emerald green, lower throat blackish, rest of underparts dull greenish grey; inner tail feathers blue-green, outer ones blackish tipped grey. Female similar to male but entirely grey below. Immature resembles adult female. Race *aurea* smaller, with upperparts more bronze or golden, less green.

Habitat. Occurs in open understorey of higher tropical to cloudforest. Forages very low above ground. Occasionally seen at forest edges, but



rare in open vegetation. Most numerous at c. 1000-2200 m.

Food and Feeding. Nectar of flowering Rubiaceae, Verbenaceae, Oenotheraceae. Feeds on insects by hawking. Male defends nectar-rich flower stands.

Breeding. Feb-Mar. Deep, cup-shaped nest constructed of soft plant fibre and cobweb on vertical shoots at 2-3 m. No further data available.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Common resident on the Atlantic and Pacific slopes. Appears to have declined locally in N Oaxaca, Mexico, due to habitat destruction by logging. Regularly recorded at Valle Nacional, Lagos de Montebello and El Triunfo Biosphere Reserve (Mexico).

Bibliography. Anon. (1998a), Binford (1989), Friedmann *et al.* (1950), González-García (1993), Howell & Webb (1995a), Johnsgard (1997), Land (1970), Miller & Griscom (1925b), Monroe (1968), Paynter (1957), Ridgway (1911), Stotz *et al.* (1996), Wagner (1946a, 1957b).



Genus *LOPHORNIS* Lesson, 1829

73. Tufted Coquette

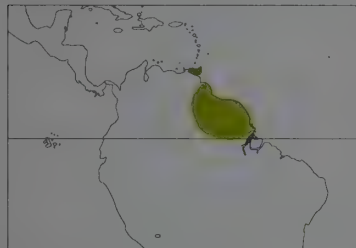
Lophornis ornatus

French: Coquette huppe-col **German:** Schmuckelfe
Other common names: Splendid Coquette

Spanish: Coqueta Adornada

Taxonomy. *Trochilus ornatus* Boddaert, 1783, Cayenne. Monotypic.

Distribution. E Venezuela, Trinidad and the Guianas to N Brazil.



Descriptive notes. 6-8-7 cm; 2.3-2.8 g. Male has short straight bill, red, tipped black; forehead iridescent green, crest long, dark rufous, rest of upperparts shining pale green, rump with buffy white band, uppertail-coverts purplish; long tufts (elongated feathers springing fan-like from cheeks) rufous, each with green iridescent spot at distal end, throat glittering emerald-green, rest of underparts pale green; tail squared, central rectrices bronzy-green, remainder rufous with bronzy-green tips and edges. Female lacks crest and tufts, rump buff; underparts rufous, with green flanks. Immature resembles adult female.

Habitat. Edges of humid forest, gallery forest, thickets, cultivated areas like plantations, and savannas, at 100-1000 m.

Food and Feeding. Feeds on arthropods and on nectar of flowering Acanthaceae, Asclepiadaceae (*Asclepias*), Compositae, Euphorbiaceae, Labiatae, Marantaceae, Myrtaceae, Rubiaceae and Verbenaceae (*Stachytarpheta*). Feeds by trap-lining.

Breeding. Dry season in Trinidad, Jan-Apr; Dec-Mar in Guyana. Nest cup-shaped, built out of fine and soft plant fibres, placed c. 2 m above ground. Clutch size 2; incubation by female 13-14 days; fledging at 20 days.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Common. Accepts man-made habitats like plantations. Occurs in several protected areas such as Paria Peninsula National Park (Venezuela) and Asa Wright Nature Centre (Trinidad). Regularly recorded in Kanuku Mts of SW Guyana. During recent decades has been imported into Europe for wild bird trade but this has now been ended.

Bibliography. Allen (1961), Bangs & Penard (1918), Berlepsch (1908), Chubb (1916), Cordier (1982), French (1991), Gilliard (1941), Grantsau (1988), Haverschmidt & Mees (1994), Herklots (1961), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Olrog (1968), Ruschi (1981-1982, 1982a, 1986), Schuchmann-Wegert & Schuchmann (1986), Sick (1993, 1997), Snyder (1966), Stotz *et al.* (1996), Tostain *et al.* (1992).

74. Dot-eared Coquette

Lophornis gouldii

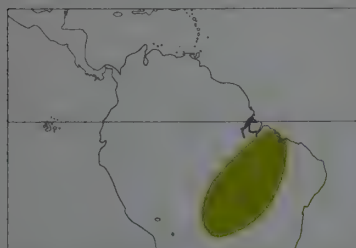
French: Coquette de Gould

German: Gouldelfe

Spanish: Coqueta Moteada

Taxonomy. *Ornismya gouldii* Lesson, 1833, no locality. Monotypic.

Distribution. NC & C Brazil (Pará and Maranhão to Mato Grosso and Goiás) to E Bolivia (Santa Cruz).



Descriptive notes. 6-8-7.6 cm; 2.5-2.8 g. Male has short straight bill, red, tipped black; forehead glittering golden green, crest dark rufous, remainder of upperparts bronzy-green, white band across rump; throat glittering emerald-green, tufts (elongated feathers springing fan-like from cheeks) white with shining green spots distally, rest of underparts greyish-green; tail squared, central rectrices bronzy-green, remainder rufous with bronzy-green tips and edges. Female lacks tufts and crest; similar to male above, but with more bronze iridescence; throat rufous, below washed greyish-green; tail square, dark bronze distally rufous. Immature resembles adult female.

Habitat. Forest edges, savanna and *cerrado* up to 500 m.

Food and Feeding. No specific data available. Presumably feeds on nectar of similar flowers visited by *L. ornatus*; trap-liner.

Breeding. Dec-Apr. Nest undescribed; clutch size 2; incubation 14 days, by female; fledging period 22 days.

Movements. No information; presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. No life-history data available; may take to man-made habitats to some extent. Occurs in Chapada dos Guimarães National Park, Mato Grosso (WC Brazil). Frequently recorded in Serra dos Carajás, Pará (NC Brazil).

Bibliography. Berlioz (1964), Forrester (1993), Grantsau (1988), Meyer de Schauensee (1982), Olrog (1968), Remsen & Traylor (1989), Ruschi (1953a, 1967a, 1981-1982, 1982a, 1986), Schuchmann-Wegert & Schuchmann (1986), Sick (1993, 1997), Stotz *et al.* (1996), Wilkinson (1996).

75. Frilled Coquette

Lophornis magnificus

French: Coquette magnifique

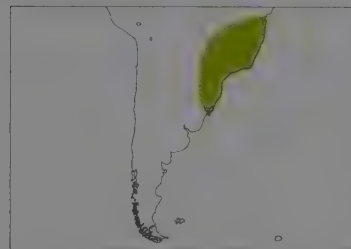
German: Prachtelfe

Spanish: Coqueta Magnífica

Taxonomy. *Trochilus magnificus* Vieillot, 1817, Brazil.

Monotypic.

Distribution. CE Brazil, from Espírito Santo S to Santa Catarina, and W to Goiás and Mato Grosso; irregularly N to Alagoas, where status uncertain.



Descriptive notes. 7.1-7.7 cm; c. 3 g, records of 1-2 and 1-8 g presumably referring to juveniles. Male has short straight bill, red, tipped black; forehead iridescent green, crest rufous, rest of upperparts bronzy-green, white band across rump; throat glittering emerald green, tufts (elongated feathers fanning out from cheeks and side of throat) shorter than in *L. gouldii*, fan-shaped, white with shining green distal band, rufous at base; rest of underparts greyish-green; tail squared, central rectrices bronzy green, remaining rufous with bronzy green tips and edges. Female lacks tufts and crest, upperparts similar to male; throat and crest, below washed greyish-green; tail squared,

with rufous discs and some white with dark crescents, below washed greyish-green; tail squared, dark bronzy, distally rufous. Immature resembles adult female.

Habitat. Edges of humid forest, second growth, coffee plantations, and *cerrado* up to 1000 m.

Food and Feeding. Feeds on arthropods and nectar of small flowering plants like *Cirrus*, *Duranta arborensis*, introduced *Eucalyptus*, *Genipa americana*, *Hibiscus*, *Inga affinis*, *Lantana camara*, *L. lilacina*, *L. brasiliensis*, *Leonurus siribicus*, *Myrciaria cauliflora*, *Palicourea*, *Psychotria maregravii*, *Tilandsia*. Subordinate to other larger hummingbirds.

Breeding. Aug-Mar. Cup-shaped nest built out of fine plant down and moss, decorated with green and whitish lichens on the outside, 2-5 m above ground, saddled on branches in bushes or small trees. Clutch size 2; incubation 12-13 days by female; fledging at 20 days.

Movements. Some seasonal dispersal, possibly following flowering and reproductive season.

Status and Conservation. Not globally threatened. CITES II. Common. Readily accepts man-made habitats like plantations and flowering gardens and other disturbed areas like second growth. Occurs in Nova Lombardia and Santa Lúcia Biological Reserves (Espírito Santo); also recorded in Pedra Talhada State Park (Alagoas). Many individuals imported to Europe over recent decades for cage-bird trade; importation now under national and international regulations.

Bibliography. de Almeida & Ruschi (1976), Belton (1984), Dubs (1992), Forrester (1993), Grantsau (1988), Mobbs (1972a), Oniki (1996), Oniki & Willis (1998), Parker & Goerck (1997), do Rosário (1996), Ruschi (1949b, 1973d, 1981-1982, 1982a, 1982b, 1986), Rutgers & Norris (1972), Sargeant (1996), Schuchmann-Wegert & Schuchmann (1986), Scott & Brooke (1985), Sick (1993, 1997), Sick & Pabst (1968), Stotz *et al.* (1996), Teixeira *et al.* (1987), Tobias *et al.* (1993), Wittmann (1982).

76. Short-crested Coquette

Lophornis brachylophus

French: Coquette du Guerrero

German: Kurzhaubenelfe

Spanish: Coqueta de Guerrero

Taxonomy. *Lophornis delattrei brachylophus* R. T. Moore, 1949, San Vicente de Benítez, Guerrero, Mexico. Forms a superspecies with *L. delattrei* and possibly *L. stictolophus*; has been considered conspecific with former. Monotypic.

Distribution. Sierra Madre del Sur in Guerrero (SW Mexico).



Descriptive notes. 7-7.5 cm. Male has short, straight bill, black; crest short (c. 1-2 cm), filamentous, rufous, longest feathers tipped green; rest of upperparts deep emerald green, white band across rump, lower rump bronzy-purple, uppertail-coverts green; throat iridescent emerald green, cheek tufts not as conspicuous as in other congeners, short, rufous with iridescent green distal band; whitish band below throat, rest of underparts pale cinnamon; tail double-rounded, central pair of rectrices green, remainder cinnamon-rufous, tipped black. Female lacks crest and tufts, forehead dull cinnamon, upperparts pale green; buffy to whitish

band across rump, lower rump duller; throat whitish, bordered by white band, lower underparts pale cinnamon; tail rounded, central pair of rectrices green, tipped blackish, others cinnamon with blackish subterminal bar, tips pale buff. Immature resembles adult female.

Habitat. Semi-deciduous forest, humid evergreen forest, pine-oak forest, and plantations at 900-1800 m.

Food and Feeding. Feeds on nectar of flowering *Cecropia*, *Clethra*, *Conostegia*, *Inga* and other small flowering plants. Hawks in the air for arthropods.

Breeding. Probably Nov-Feb. No further data available.

Movements. Sedentary with some altitudinal movements likely.

Status and Conservation. **ENDANGERED.** CITES II. Restricted-range species; present in Sierra Madre del Sur EBA. Rare to locally common. Species is restricted to a small area about 40 km across, and it is only recorded frequently between the villages of Arroyo Grande, Paraíso and Nueva Delhi, Guerrero. The habitat is unprotected and under severe threat of deforestation for agricultural purposes such as corn and coffee cultivation. To date no plans exist for the protection of this forest type.

Bibliography. Anon. (1998a), Banks (1990), Blake (1953), Ceballos-Lascurain (1989), Collar *et al.* (1992), Friedmann *et al.* (1950), Hernández-Baños *et al.* (1995), Howell (1989a, 1989c, 1992), Howell & Webb (1995a), Johnson (1997), Moore (1949), Navarro (1992), Navarro *et al.* (1991), Ornelas (1987), Schuchmann (1990b), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Wege & Long (1995).

77. Rufous-crested Coquette

Lophornis delattrei

French: Coquette de Delattre

German: Zierelfe

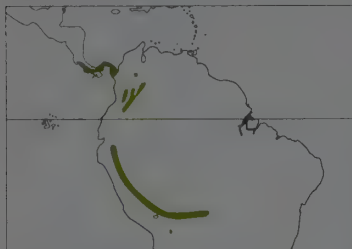
Spanish: Coqueta Crestirrufa

Other common names: Dusky Coquette ("melanie")

Taxonomy. *Ornismya* (*Lophorinus*) *DeLattrei* Lesson, 1839, no locality = Moyobamba, Peru. Forms a superspecies with *L. brachylophus* and possibly *L. stictolophus*; has been considered conspecific with former. Proposed species "*L. melaniae*", apparently from Colombia, probably represents aberrant individuals or faded skins of present species; it is not, as previously reported, melanistic. Bolivian birds were tentatively split as race *regulus*, but, despite some possible differences in female plumage, probably best treated as synonym of nominate. Two subspecies recognized.

Subspecies and Distribution.

L. d. lessoni Simon, 1921 - Pacific and Caribbean slopes of SW Costa Rica and Panama, and C & E Andes of Colombia (Magdalena Valley and Santander).
L. d. delattrei (Lesson, 1839) - E Peru and N Bolivia (to Beni and Santa Cruz).



Descriptive notes. 6.4-7 cm; c. 2.8 g. Male has short straight bill, red, tipped black; crest long (c. 2 cm) filamentous, rufous, green tips distally; rest of upperparts bronzy-green with white band across rump, lower rump and uppertail-coverts purplish-bronze; throat glittering green, cheek tufts not as conspicuous as in other congeners, rufous with broad iridescent green distal band, throat subtended by some white pointed feathers, rest of underparts bronzy green; tail double-rounded, central pair of rectrices green, remainder cinnamon-rufous, tipped black and edged green. Female lacks crest and tufts, forehead dull cinnamon-rufous, upperparts similar

to male; throat buffy to pale rufous with bronzy discs distally, rest of underparts similar to male but duller; tail rounded, central pair of rectrices green, tipped blackish, others cinnamon with blackish subterminal bar, tips pale buff. Immature resembles adult female but throat greyish. Race *lessoni* has more sharply pointed crest feathers with green almost absent, white terminal throat feathers less pointed. **Habitat.** Edges of humid forest, clearings, along roadsides, and semi-open habitats with bushes, at 600-2000 m. Forages at lower levels.

Food and Feeding. Feeds on nectar of flowering *Inga*, Myrtaceae, Verbenaceae and other small flowering plants. Arthropods are caught in the air by hawking.

Breeding. No information available; presumably breeds during drier season like congeners.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Generally rare, though not restricted to forest habitats, and therefore not affected directly by extensive deforestation within its range. Occurs in Beni Biosphere Reserve (NC Bolivia).

Bibliography. Anon. (1998a), Banks (1990), Best *et al.* (1997), Bond & Meyer de Schauensee (1943), Floerike (1920), Hilty & Brown (1986), Johnsgard (1997), Parker *et al.* (1982), Remsen & Traylor (1989), Ridgely & Gwynne (1989), Ridgway (1911), Schuchmann (1990b), Schuchmann-Wegert & Schuchmann (1986), Slud (1964), Stiles (1985c), Stiles & Skutch (1989), Stotz *et al.* (1996), Walters (1997), Wetmore (1968a), Willis & Eisenmann (1979), Zimmer (1950d).

78. Spangled Coquette

Lophornis stictolophus

French: Coquette pailletée

German: Glanzelfe

Spanish: Coqueta Coronada

Taxonomy. *Lophornis stictolophus* Salvin and Elliot, 1873, Antioquia, Colombia.

Possibly forms a superspecies with *L. brachylophus* and *L. delattrei*. "*L. insignibarb*", known from a single Bogotá trade skin and sometimes awarded monospecific genus *Lithiophanes*, may be a hybrid of present species and *L. chalybeus verreauxii*, although apparently characters do not fit precisely with either. Monotypic.

Distribution. W Venezuela through E Colombia and E Ecuador to N Peru (Marañón Valley).



Descriptive notes. 6.4-6.9 cm. Very similar to *L. delattrei*. Male has short straight bill, red, tipped black; forehead and crest rufous, crest feathers slightly shorter than in *L. delattrei*, broader, distal tips blackish, appearance of crest more bushy; rest of upperparts bronzy-green with white band across rump, lower rump and uppertail-coverts purplish-bronze; throat glittering green, cheek tufts not as conspicuous as in other congeners, rufous with broad iridescent green distal band; throat subtended by some white pointed feathers, rest of underparts bronzy-green; tail double-rounded, central pair of rectrices green, remainder cinnamon-rufous, tipped black. Female lacks crest and tufts, forehead dull cinnamon-rufous, upperparts similar to male; throat whitish with large rufous spots, belly cinnamon often with some green discs; tail rounded, central pair of rectrices green, rest cinnamon basally, all with blackish subterminal bar, tips buff. Immature resembles adult female but throat greyish.

Habitat. Edge of humid forest, clearings, *cerrado* and drier scrubby areas, up to 1300 m. Usually found below range of *L. delattrei* which it may replace ecologically.

Food and Feeding. No specific data available but possibly feeds on nectar of similar flowers as *L. delattrei*, including *Inga*, *Lantana*, Verbenaceae and Myrtaceae. Takes arthropods in the air by hawking.

Breeding. No information available.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Currently considered Near-threatened. Generally rare, but no immediate threats recorded so far. Like *L. delattrei* this species is not restricted to forest habitats and may accept man-made habitats to some extent. Recorded near Santo Domingo, Mérida (Venezuela) and at Panacocha (NE Ecuador).

Bibliography. Best *et al.* (1997), Butler (1979), Hilty & Brown (1986), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Olrog (1968), Parker *et al.* (1982), Rahbek *et al.* (1995), Schuchmann-Wegert & Schuchmann (1986), Stotz *et al.* (1996), Zimmer (1950d).

79. Festive Coquette

Lophornis chalybeus

French: Coquette chalybée

German: Schmetterlingselfe

Spanish: Coqueta Verde

Other common names: Butterfly Coquette (*verreauxii*)

Taxonomy. *Trochilus chalybeus* Vieillot, 1823, Brazil.

Together with its sister species, *L. pavoninus*, formerly placed in a separate genus, *Polemistria*. Disjunct distribution and morphological differences between S nominate and N races suggest they might be approaching species threshold. "*L. insignibarb*", known from a single Bogotá trade skin and sometimes awarded monospecific genus *Lithiophanes*, may be a hybrid of race *verreauxii* and *L. stictolophus*, although apparently characters do not fit precisely with either. Three subspecies recognized.

Subspecies and Distribution.

L. c. klagesi Berlepsch & Hartert, 1902 - SE Venezuela.

L. c. verreauxii J. Verreaux & E. Verreaux, 1853 - E Colombia, E Ecuador and E Peru to NW Brazil and C Bolivia.

L. c. chalybeus (Vieillot, 1823) - SE Brazil (Espírito Santo, Minas Gerais, Santa Catarina).



Descriptive notes. 7.6-8.5 cm; c. 3 g (record of 2.2 g presumably refers to juvenile). Male has short, straight black bill; cheeks blackish, forehead iridescent green bordered by black band consisting of stiff feathers, rest of upperparts bronzy-green with white bar across rump, lower rump and uppertail-coverts purplish-bronze; cheek tufts green tipped white, breast whitish with dark streaking, belly greyish-brown with blackish central stripe; tail purplish-copper. Female lacks tufts, upperparts like male but lacks glittering frontlet; chin whitish-buff forming a white moustachial stripe, rest of underparts brownish scaled whitish; tail similar to that of male, outer pairs of rectrices tipped greyish to buff. Immature resembles adult female. Race *verreauxii* has hindcrown elongated by filamentous feathers, green crest, throat and belly blackish-green; *klagesi* is dark green above, uppertail-coverts bronzy-olive, white tips on tufts smaller, rectrices bronzy-green, female generally darker, tips on rectrices smaller and darker.

Habitat. Humid forest, second growth and *cerrado*, at 100-1000 m.

Food and Feeding. Feeds on nectar of flowering Acanthaceae, Bromeliaceae, Compositae, Malvaceae, Myrtaceae, Rubiaceae and Vochysiaceae. Arthropods are possibly gleaned from foliage.

Breeding. Aug-Nov. Nest cup-shaped, constructed of fine soft plant down, saddled at the end of branches in small trees 2-5 m above ground. Clutch size 2; incubation period 13-14 days by female; fledging at 22 days.

Movements. Sedentary, with some seasonal short-distance dispersal most likely. Single record from NE Argentina (Buenos Aires).

Status and Conservation. Not globally threatened. CITES II. No information on abundance available. Part of habitat under threat of deforestation. Occurs in Tambopata Reserve (SE Peru) and Itatiaia and Marumbi National Parks (SE Brazil).

Bibliography. Allen (1995), Best *et al.* (1997), Bond & Meyer de Schauensee (1943), Butler (1979), Canevari *et al.* (1991), Donahue (1994), Grantsau (1988), Gyldestolpe (1945b), Hilty & Brown (1986), Meyer de Schauensee & Phelps (1978), Olrog (1972, 1979b), Parker *et al.* (1982), de la Peña (1994), Remsen & Traylor (1989), do Rosário (1996), Ruschi (1953a, 1953b, 1962c, 1981-1982, 1982a, 1986), Salvador & Salvador (1990), Schuchmann-Wegert & Schuchmann (1986), Sick (1993, 1997), Stotz *et al.* (1996), Terborgh *et al.* (1984), Zimmer (1950d).

80. Peacock Coquette

Lophornis pavoninus

French: Coquette paon

German: Pfauenelfe

Spanish: Coqueta Pavonina

Taxonomy. *Lophornis pavoninus* Salvin and Godman, 1882, Merumé Mountains, Guyana.

Together with its sister species, *L. chalybeus*, formerly placed in a separate genus, *Polemistria*. Proposed race *punctigula* (Cerro Paritepui), described on basis of slight differences in female plumage, best considered synonymous with nominate. Two subspecies recognized.

Subspecies and Distribution.

L. p. pavoninus Salvin & Godman, 1882 - Cerro Paritepui (SE Venezuela), Mt Roraima (SE Venezuela/NC Brazil) and Merumé Mts (Guyana).

L. p. duidae Chapman, 1929 - Mt Duida and adjacent smaller tepuis in SE Venezuela.



Descriptive notes. c. 9-7 cm. Male has short, straight black bill; head glittering golden green with median black line, upperparts shining dark green with white band across rump; throat black, cheek tufts broad, shining green with large blackish-blue spots at distal end, proximally rufous with white spot, rest of underparts greyish-green; tail slightly forked, purplish-bronze. Female lacks tufts; upperparts golden bronzy with buffy white band across rump; throat white with black streaks, lateral feathers elongated, black and white, rest of underparts mottled black, white and green; tail greyish with broad purplish-bronze subterminal bar, outer pair of rectrices tipped whitish. Immature resembles adult female. Race *duidae* has black median line on crown narrow; rufous at base of cheek-fans reduced, and lacks white.

Habitat. Rainforest, cloudforest, clearings and forest edge, at 500-2000 m. Forages alone or in small groups in canopy.

Food and Feeding. Feeds on nectar of flowering *Inga*, *Lantana*, *Rubus*, *Salvia*, Bromeliaceae, Rutaceae and Compositae. Arthropods are possibly gleaned from foliage.

Breeding. No information on season; nest cup-shaped, suspended on horizontal branches c. 2 m above ground. Clutch size 2; incubation 13-14 days, by female; fledging at 20 days.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Tepuis EBA. Forest habitat on top of tepuis still remain pristine. However, during the last few years adventure tourism, including para-gliding, on Mt Roraima and other tepuis has increased steadily, but so far no immediate threat has been detected. Present species seems not to inhabit man-made habitats and other disturbed areas. Frequently recorded in the Escalera area, Bolívar (S Venezuela).

Bibliography. Chapman (1929), Chubb (1916), Dickerman & Phelps (1982), Forrester (1993), Grantsau (1988), Mayr & Phelps (1967), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Olrog (1968), Ruschi (1981-1982, 1982a, 1986), Schuchmann-Wegert & Schuchmann (1986), Sick (1993), Snyder (1966), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Zimmer & Phelps (1946).

81. Black-crested Coquette

Lophornis helenae

French: Coquette d'Hélène **German:** Schwarzschoepfelfe **Spanish:** Coqueta Crestinegra
Other common names: Princess Helena's Coquette

Taxonomy. *Ornismya Helena* DeLattre, 1843, Vera Paz, Guatemala. Together with its sister species, *L. adorabilis*, formerly placed in a separate genus, *Paphosia*. Monotypic.

Distribution. S Mexico (Veracruz, Oaxaca, Chiapas) S to E Costa Rica.



Descriptive notes. 6.4-7 cm; male and female 2.6-2.8 g. Male has short straight bill, red, tipped black; crown iridescent green, wispy crest hair-like, black, rest of upperparts bronzy-green with whitish band across rump, lower rump blackish; throat iridescent green, breast black, elongated lateral feathers buff on inner web, bronzy breast band, belly white with large iridescent bronzy discs; tail slightly forked, central rectrices dark green, remainder rufous, edged dusky green. Female lacks crest, upper mandible black, lower red, tipped black; head blackish, cheeks black, upperparts bronzy-green with buffy white band across rump, lower

rump blackish; throat buffy white with bronzy discs, rest of underparts whitish with large bronzy discs, undertail-coverts cinnamon; tail rounded, dusky green, subterminal bar blackish, outer rectrices tipped cinnamon. Immature resembles adult female.

Habitat. Semi-open habitats, forest edge, second growth, gaps and plantations at 100-1200 m. Forages usually at canopy level.

Food and Feeding. Feeds on nectar of flowering *Clusia*, *Cordia*, *Dipteryx*, *Hampea*, *Hymenolobium*, *Norantea* and *Vochysia*. Gleans arthropods from foliage and twigs. Subordinate to other larger hummingbirds; feeds using trap-lining technique.

Breeding. Nest found in Mar; small, cup-shaped at end of twig 8 m above ground. No further information available.

Movements. Sedentary, with irregular seasonal altitudinal dispersal.

Status and Conservation. Not globally threatened. CITES II. Generally uncommon. May accept man-made habitats like plantations to some extent. Species has been recorded in Sierra de Los Tuxtlas (Veracruz), and at Lagos de Montebello and on the Mayan ruins of Bonampak (Chiapas).

Bibliography. Anon. (1998a), Barlow *et al.* (1969), Binford (1989), Brown & Bowers (1985), Fogden (1993), Friedmann *et al.* (1950), González-García (1993), Howell & Webb (1995a), Johnsgard (1997), Land (1970), Monroe (1968), Rangel-Salazar (1990), Ridgway (1911), Schuchmann-Wegert & Schuchmann (1986), Slud (1964), Stiles (1985b, 1985c), Stiles & Skutch (1989), Stotz *et al.* (1996).

82. White-crested Coquette

Lophornis adorabilis

French: Coquette adorable **German:** Weißschoepfelfe **Spanish:** Coqueta Adorable
Other common names: Adorable Coquette

Taxonomy. *Lophornis adorabilis* Salvin, 1870, Bugaba, Chiriquí. Together with its sister species, *L. helenae*, formerly placed in a separate genus, *Paphosia*. Monotypic.

Distribution. C Costa Rica to W Panama.



Descriptive notes. 7-7.8 cm; c. 2-7 g. Male has short straight bill, red, tipped black; bill heavier than those of congeners; forehead fiery coppery, crest white, rest of upperparts bronzy-green with buffy white band across rump, lower rump and uppertail-coverts purplish-bronzy; throat and hair-like elongated tufts glittering green, breast white, rest of underparts cinnamon-rufous with some green discs on flanks; tail forked, rufous chestnut edged bronzy-green. Female lacks crest and tufts, upper mandible black, lower red, tipped black, upperparts similar to male, slightly duller, black mask; throat and breast white with small bronzy green

discs, rest of underparts cinnamon-rufous; tail has subterminal blackish band. Immature resembles adult female; immature male has some green discs on throat.

Habitat. Humid forest, forest edge, second growth and shaded plantations, at 300-1200 m. Usually forages at canopy level, occasionally descends to lower strata while feeding in second growth and at edges.

Food and Feeding. Feeds on nectar of flowering *Inga*, *Lonchocarpus*, *Stachytarpheta* and *Vochysia*. Arthropods are gleaned from foliage and twigs. Dominated by larger hummingbird species; feeds by trap-lining.

Breeding. Dec-Feb. Nest cup-shaped, constructed of soft plant down, decorated with lichens on exterior, 5-20 m above ground, exposed at end of twigs at forest edge or clearings. Clutch size 2; incubation by female but no exact data on incubation period; fledging at 21-22 days.

Movements. Sedentary, with seasonal altitudinal dispersal.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in South Central American Pacific Slope EBA. Locally common. Takes to man-made habitats such as plantations; not confined to forest habitat which is under some threat of deforestation. No immediate threat so far recorded.

Bibliography. Anon. (1998a), Johnsgard (1997), Ridgely & Gwynne (1989), Schuchmann-Wegert & Schuchmann (1986), Skutch (1961a), Slud (1964), Stattersfield *et al.* (1998), Stiles (1985c), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968a).

PLATE 52

inches 2
cm 5



Genus *DISCOSURA* Bonaparte, 1850

83. Wire-crested Thorntail

Discosura popelairii

French: Coquette de Popelaire **German:** Haubenfadenelfe **Spanish:** Rabudito Crestado
Other common names: Popelaire's Coquette

Taxonomy. *Trochilus popelairii* Du Bus de Gisignies, 1846, Peru. Often placed in genus *Popelairia*, along with *D. langsdorffi*, *D. letitia* and *D. conversii*; genus closely related to *Lophornis*. Monotypic.
Distribution. E Colombia, E Ecuador and NE Peru.



Descriptive notes. Male c. 11.4 cm (including long tail), female 7.5-8.2 cm; c. 2.5 g. Male has short straight black bill; crown glittering green with long narrow hair-like crest, rest of upperparts coppery green with white band across rump; gorget iridescent green, underparts black, sides brownish with white patch on flanks; tail long, forked, steely blue, outer rectrices narrow, shafts of all rectrices white. Female upperparts similar but lacking crest; underparts black with white malar streak and patch on flanks; tail short, slightly forked, bluish-black, tipped white. Immature resembles adult female.

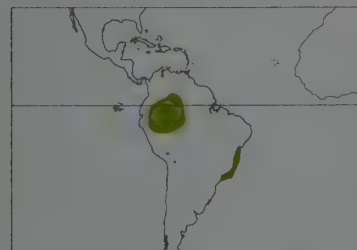
Habitat. Humid forest and edges at 500-1200 m. Usually forages in canopy.
Food and Feeding. Feeds on nectar of flowering *Inga* trees; also takes arthropods.
Breeding. One nest in Apr (Colombia) saddled at end of branch 8 m above ground.
Movements. No information available. Probably sedentary.
Status and Conservation. Not globally threatened. CITES II. Generally rare. Does not seem partial to man-made habitats; habitat within range under severe threat of destruction. In NE Ecuador, regularly recorded between Tena and Coca.
Bibliography. Best *et al.* (1997), Bloch *et al.* (1991), Butler (1979), Cordier (1982), Hilty & Brown (1986), Meyer de Schauensee (1966, 1982), Olrog (1968), Parker *et al.* (1982), Salaman & Mazariegos (1998a, 1998b), Schuchmann (1976a), Stotz *et al.* (1996), Taczanowski (1884), Terborgh *et al.* (1984), Williams & Tobias (1994), Wittmann (1982).

84. Black-bellied Thorntail

Discosura langsdorffi

French: Coquette de Langsdorff **German:** Brustband-Fadenelfe **Spanish:** Rabudito Ventrinegro
Other common names: Black-breasted/Langsdorff's Thorntail

Taxonomy. *Trochilus langsdorffi* Temminck, 1821, Brazil. Often placed in genus *Popelairia*, along with *D. popelairii*, *D. letitia* and *D. conversii*; genus closely related to *Lophornis*. Two subspecies recognized.
Subspecies and Distribution.
D. l. melanosternon (Gould, 1868) - SE Colombia and S Venezuela to E Ecuador, E Peru and W Brazil (R Madeira, R Guaporé, R Negro, W Mato Grosso).
D. l. langsdorffi (Temminck, 1821) - E Brazil (Bahia, Espírito Santo, Rio de Janeiro).



Descriptive notes. Male 12-13.7 cm (including long tail), female 7-6 cm; c. 3-2 g. Male has short straight black bill; crown iridescent emerald green, rest of upperparts coppery green with white band across rump; gorget iridescent emerald green, bordered by a golden coppery band, belly black, flanks bronzy-green; tail long, forked, outer rectrices narrow, outer 3 pairs of rectrices grey, shafts of all rectrices white. Female has upperparts similar to male; throat white spangled green and black, small white malar streak, breast spangled green with lower border coppery, belly black with white patch on flanks; tail short and forked, basally

bronze, rest steely blue tipped white. Immature resembles adult female. Race *melanosternon* slightly smaller, with crown grass green, underparts darker, more golden on breast.

Habitat. Humid lowland forest and edges, at 100-300 m. Forages from mid-strata to canopy.
Food and Feeding. Feeds on arthropods and nectar of flowering *Calliandra*, *Inga* trees, *Lantana*, *Mimosa*, *Vochysia*, Bromeliaceae, Compositae, Labiatae, Fabaceae, Malvaceae and Rubiaceae.
Breeding. Nov-Mar. Nest cup-shaped, made out of the soft down of *Typha*, bromeliads and other plant seeds, externally decorated with pieces of lichen; placed on horizontal branch c. 10 m above ground. Clutch size 2; incubation 13 days, by female; fledging at 20 days.
Movements. No information available. Probably sedentary.
Status and Conservation. Not globally threatened. CITES II. Generally considered rare throughout range. Habitat under severe threat of deforestation, and species does not seem to accept man-made habitats. Protected locally in some national parks. Regularly recorded at Panacocha (E Ecuador).
Bibliography. Best *et al.* (1997), Butler (1979), Grantsau (1988), Hilty & Brown (1986), Meyer de Schauensee & Phelps (1978), O'Neill (1974), Parker & Goerck (1997), Parker & Remsen (1987), Parker *et al.* (1982), Remsen & Traylor (1989), Ruschi (1973d, 1981-1982, 1982a, 1986), Salaman & Mazariegos (1998a), Sargeant (1996), Stotz, Fitzpatrick *et al.* (1996), Stotz, Lanyon *et al.* (1997), Taczanowski (1884), Zimmer & Hilty (1997), Zimmer *et al.* (1997).

85. Coppery Thorntail

Discosura letitia

French: Coquette de Létitia **German:** Kupferfadenelfe **Spanish:** Rabudito Cobrizo

Taxonomy. *Trochilus letitia* Bourcier and Mulsant, 1852, Bolivia. Often placed in genus *Popelairia*, along with *D. popelairii*, *D. langsdorffi* and *D. conversii*; genus closely related to *Lophornis*. Monotypic.
Distribution. Lowlands of NE Bolivia.



Descriptive notes. c. 9 cm. Male has short, straight black bill, crown iridescent emerald green, rest of upperparts bronzy-green with white band across rump; gorget iridescent emerald green, belly dusky washed with green, flanks bronzy-green; tail long, forked, outer rectrices narrow, purplish-black, shafts of all rectrices whitish. Female unknown.

Habitat. Probably rainforest along rivers.
Food and Feeding. No information available; most likely feeds on nectar of same flowers as congeners.
Breeding. No information available.
Movements. No information available.

Status and Conservation. Not globally threatened. Data-deficient. CITES II. Restricted-range species; precise distribution uncertain. Possibly extinct. Has not been recorded during this century and is known only from three 19th-century specimens. Possibly the least known of all hummingbird species. Urgent action required to verify distributional range and gather information on its life history.

Bibliography. Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Ergueta & de Morales (1996), Meyer de Schauensee (1982), Olrog (1968), Remsen & Traylor (1989), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Wege & Long (1995).

86. Green Thorntail

Discosura conversii

French: Coquette à queue fine **German:** Grüne Fadenelfe **Spanish:** Rabudito Verde

Taxonomy. *Trochilus Conversii* Bourcier and Mulsant, 1846, Bogotá. Often placed in genus *Popelairia*, along with *D. popelairii*, *D. langsdorffi* and *D. letitia*; genus closely related to *Lophornis*. Monotypic.
Distribution. Costa Rica and Panama through W Colombia to W Ecuador.



Descriptive notes. Male c. 10 cm (including long tail), female c. 6-6.7-5 cm; c. 3 g. Male has short, straight bill, black; crown glittering green, rest of upperparts green with white band across rump; underparts shining green with blue centre to breast and white flank patch; tail long, forked, steely blue, outer rectrices narrow, shafts of all rectrices white. Female upperparts similar to male; blackish below with some green discs, white malar streak, green breast band; tail shorter, forked, black, tipped white. Immature resembles adult female.

Habitat. Humid forest, forest edge and at flowering trees in clearings up to 1000 m, occa-

sionally 1400 m. Forages from mid-strata to canopy.

Food and Feeding. Feeds on nectar of flowering *Clusia*, *Inga*, *Mimosa*, *Pithecollobium* and *Warszewiczia*. Gleans insects and spiders from undersurface of larger canopy leaves.

Breeding. Probably Nov-Apr (Costa Rica). No further information available.
Movements. Sedentary, some seasonal altitudinal dispersal likely.

Status and Conservation. Not globally threatened. CITES II. Uncommon throughout most of range. In common with congeners, restricted to forest habitats which remain under threat of deforestation; does not seem to accept man-made habitats. Species occurs in several protected areas, e.g. Tapantí National Park, Costa Rica. In Ecuador, regularly recorded along old Santo Domingo road and at Tinalandia.

Bibliography. Anon. (1998a), Best *et al.* (1997), Butler (1979), Fogden (1993), Hilty (1997), Hilty & Brown (1986), Kirwan & Marlow (1996), Ridgely & Gwynne (1989), Rutgers & Norris (1972), Salaman & Mazariegos (1998b), Slud (1960, 1964), Stiles (1980, 1985b), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968a), Williams & Tobias (1994).

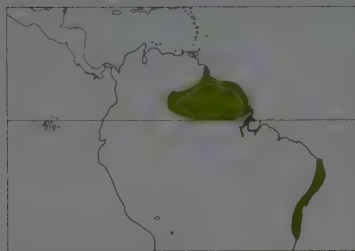
87. Racquet-tailed Coquette

Discosura longicauda

French: Coquette à raquettes **German:** Diskuselfe **Spanish:** Rabudito de Raquetas
Other common names: Brazilian Racquet-tail, Racquet-tailed Hummingbird

Taxonomy. *Trochilus longicauda* J. F. Gmelin, 1788, no locality = Cayenne. Often treated as sole member of genus *Discosura*, the remaining species being separated off in *Popelairia*; genus closely related to *Lophornis*. Monotypic.
Distribution. S Venezuela (Amazonas, Bolívar) and the Guianas to NC Brazil (N Amazonas to Amapá); also NE Brazil (Rio Grande do Norte to Espírito Santo).

Descriptive notes. Male c. 10 cm (including long tail), female c. 7-8 cm; 3-3.7 g. Male has short straight black bill; crown iridescent green, rest of upperparts bronzy-green with buffy white band across rump; throat glittering emerald green, lower breast golden-coppery, belly whitish; tail long, forked, purplish, outer pair of rectrices terminating in a blackish racquet. Female upperparts similar



to male, lacks iridescent parts; throat black, laterally bordered white, breast green, belly buffy white; tail moderately long, slightly forked, grey, subterminal bar dark purple, outer rectrices tipped white. Immature resembles adult female.

Habitat. Humid forest along rivers up to 200 m altitude and scrubby savanna. Forages mainly in canopy.

Food and Feeding. Feeds on nectar of flowering *Anacardium*, *Calliandra*, *Inga*, introduced *Eucalyptus*, *Leonotis*, *Leonurus*, Lorantheaceae, Vochysiaceae, Verbenaceae. Arthropods are gleaned from foliage and spiders' webs.

Breeding. No information on season. Nest cup-shaped, made out of soft plant material, lined with *Typha* seed down, fibres of Bromeliaceae and Gramineae; placed 3-6 m above ground on horizontal branch. Clutch size 2; incubation 13-14 days, by female; fledging period 20-22 days.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Rare throughout range. Affected by extensive deforestation in many parts of range, most of which is unprotected; however, species occurs in some protected areas such as Imataca Forest Reserve, Bolívar (Venezuela), and Monte Pascoal National Park, Bahia (Brazil). Does not adapt to man-modified habitats.

Bibliography. Berlepsch (1908), Boesman (1998), Chubb (1916), Forrester (1993), Friedmann (1948), Grantsau (1988), Haverschmidt & Mees (1994), Meyer de Schauensee & Phelps (1978), Ruschi (1953b, 1973d, 1981-1982, 1982a, 1986), Rutgers & Norris (1972), Sargeant (1996), Sick (1993, 1997), Snyder (1966), Stotz *et al.* (1996), Tostain *et al.* (1992).

Genus *TROCHILUS* Linnaeus, 1758

88. Red-billed Streamertail

Trochilus polytmus

French: Colibri à tête noire

Spanish: Colibri Portacintas Piquirrojo

German: Rotschnabel-Jamaikasylyphe

Other common names: Jamaican Doctor Bird, Western Streamertail (Hummingbird)

Taxonomy. *Trochilus Polytmus* Linnaeus, 1758, Jamaica.

Genus closely related to *Chlorostilbon*. Forms a superspecies with *T. scitulus*, with which formerly considered conspecific, but differs in display and voice; occasional hybridization in W John Crow Mts. Monotypic.

Distribution. Jamaica (except extreme E).



Descriptive notes. Male 22-30 cm (including bill 2.3 cm, tail 13-17 cm), 5-2 g; female 10-5 cm, 4-4 g. Male has straight bill, coral red tipped black; head black, lateral crown feathers and ear-coverts elongated beyond nape; body iridescent emerald green, darker on back; tail black, forked, second outermost tail feather very long (streamers), scalloped and fluted on the inside; streamers of perched birds are crossed. Female's bill similar to male's, but duller red, with distal part black; above green; underparts white, lightly spotted on sides of breast and belly; tail centrally green, rest dark blue with contrasting broad white tips, no

streamers. A male morph with red chin has occasionally been found in district of St Andrews (EC Jamaica). Immature has black upper mandible, red only at base of bill; red on bill increases with age; head brownish in immature female.

Habitat. Occurs from sea-level to elfin forest and found in all man-made habitats; forages mainly throughout mid-strata and at forest edge. Most numerous at c. 1000 m; most birds at higher altitudes are not currently breeding.

Food and Feeding. Forages for nectar at native and introduced flowers, including *Hohenbergia*, *Bauhinia*, *Meriania*, *Tecoma*, *Besleria*, *Psychotria*, *Erythrina*, *Eucalyptus*, *Spathodea* and *Calliandra*, generally at height of 2-4 m. Utilizes nectar of large garden flowers by means of holes in corollas pierced by Bananquits (*Coereba flaveola*); also inspects fresh Yellow-bellied Sapsucker (*Sphyrapicus varius*) holes in trunks. Feeds on insects in the air, and takes them also from leaves, flowers, branches or spider webs.

Breeding. Breeds all year round but chiefly from Jan to mid-May. Cup-shaped nest of fine plant fibres and cobweb, with lichen attached to outer wall, placed on thin twig 1-3 m above ground. Clutch size 2; incubation 17-19 days, by female; chick black with two dorsal rows of pale grey down; fledging period 19-24 days; young remain with female for 3-4 weeks; up to 3 broods per year. First breeding in second year.

Movements. Individuals disperse to higher altitudes after main breeding season.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Jamaica EBA. Common resident. Particularly common in Blue Mts, with densities of at least 12 pairs/km². Widespread throughout most of the island, occurring at all altitudes and in all habitat types; ready occupation of man-made habitats suggests that habitat loss is unlikely to be a problem. Trapping for wild bird trade was significant until 1960's, but has now apparently stopped.

Bibliography. Allen (1961), Anon. (1998a), Blake, C.H. (1956), Bond (1985), Danforth (1928), De Quincey (1960), Douglas & Levy (1996), Downer (1972), Downer & Sutton (1990), Evans, M.R. *et al.* (1994, 1995), Gill *et al.* (1973), Gosse (1847), Krüger *et al.* (1982), Lack (1976), Leck (1974), Lodge (1896), Raffaele *et al.* (1998), Reuther (1959), Rutgers & Norris (1972), Salmon (1972), Schuchmann (1977c, 1978, 1979g, 1980a, 1980b, 1980c, 1983b, 1990a), Schuchmann & Prinzinger (1987), Schuchmann & Schmidt-Marloh (1979a, 1979b), Schürer & Bock (1983), Spence (1978), Stattersfield *et al.* (1998), Stedman, H. (1965), Stedman, V. (1974), Stotz *et al.* (1996), Tyrrell & Tyrrell (1990), Witt (1980).

89. Black-billed Streamertail

Trochilus scitulus

French: Colibri à bec noir

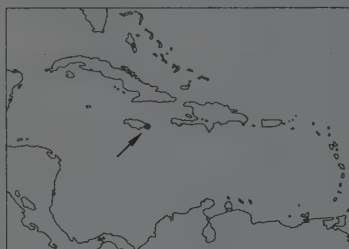
German: Schwarzschnabel-Jamaikasylyphe

Spanish: Colibri Portacintas Piquinegro

Other common names: Eastern Streamertail (Hummingbird), Doctor Bird, Scissor Tail

Taxonomy. *Aithurus scitulus* Brewster and Bangs, 1901, Priestman's River, Portland Parish, Jamaica. Genus closely related to *Chlorostilbon*. Forms a superspecies with *T. polytmus*, with which formerly considered conspecific, but differs in display and voice; occasional hybridization in W John Crow Mts. Monotypic.

Distribution. Extreme E Jamaica.



Descriptive notes. Male 22-35 cm (including bill 2.2 cm, tail 16-24 cm), 5-3 g; female 10-5 cm, 4-3 g. Male very similar to that of *T. polytmus*, but slightly smaller (except for streamers), with bill black; duller green overall, less yellow tinge to underparts, less bronzy tinge to upperparts. Female very similar to that of *T. polytmus*, but bill all black.

Habitat. Wet E Jamaica from sea-level (Port Antonio) to elfin forest (John Crow Mts). Most abundant in semi-open areas like parks, banana plantations and mountain ridges. Rarely inside dense vegetation.

Food and Feeding. Habits very similar to

those of *T. polytmus*.

Breeding. Nests all year round, chiefly Feb-Jun. Cup-shaped nest of fine rootlets and fibres is more loosely built than that of *T. polytmus*, apparently an adaptation to high precipitation; often placed on thin branches sheltered by large leaves. Clutch size 2; incubation 17-20 days, by female; chick darkish, two rows of pale grey dorsal down; fledging period 17-19 days; young remain with female for 3-4 weeks; up to 2 broods per year. First breeding in second year.

Movements. Insufficiently known, densities increase in Aug at higher altitudes around 800-1000 m.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Jamaica EBA. Common resident, but less numerous than *T. polytmus*. Particularly common around Port Antonio and Bath, with densities of at least 3-6 pairs/km². Ready occupation of man-made habitats means that habitat loss is unlikely to be a threat, but range tiny.

Bibliography. Anon. (1998a), Bond (1985), Danforth (1928), Downer & Sutton (1990), Gill *et al.* (1973), Lack (1976), Lodge (1896), Raffaele *et al.* (1998), Schuchmann (1977d, 1978, 1979g, 1980a, 1980b, 1980c, 1990a), Schuchmann & Jakob (1981a), Schuchmann & Schmidt-Marloh (1979a, 1979b), Spence (1978), Stattersfield *et al.* (1998), Tyrrell & Tyrrell (1990).

Genus *CHLOROSTILBON* Gould, 1853

90. Blue-chinned Sapphire

Chlorostilbon notatus

French: Colibri à menton bleu

Spanish: Esmeralda Gorgiazul

German: Blaukinn-Smaragdkolibri

Other common names: Audebert's Hummingbird

Taxonomy. *Trochilus notatus* Reich, 1793, Cayenne.

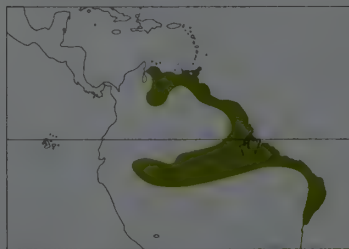
Formerly placed in monospecific genus *Chlorestes*, but morphology and bioacoustics indicate that merging into *Chlorostilbon* is more appropriate. Author and year of scientific description of species have consistently been misquoted. Racial variation complex and possibly not constant; intermediate populations exist. Birds of Brazil S of Amazon formerly awarded race *cyanogenys*. Two highly doubtful forms known only from trade skins (one and two respectively) from Bahia: "*C. subcaeruleus*" is probably a hyperchromatic aberration of present species; "*C. hypocyaneus*" may be a mutant of present species, or hybrid of present species with *Hylocharis cyanus*, or possibly even a valid species. Also, "*Eucephala scapulata*", known from single specimen from French Guiana, is probably a hybrid of present species with *Thalurania furcata*. Three subspecies currently recognized.

Subspecies and Distribution.

C. n. notatus (Reich, 1793) - NE Colombia through N & E Venezuela, Trinidad and Tobago, and the Guianas to E Brazil (Pará to Bahia).

C. n. puruensis Riley, 1913 - NW Brazil (N of Amazon, E to mouths of R Trombetas and R Negro) to SE Colombia and NE Peru (upper R Ucayali).

C. n. obsoletus (Zimmer, 1950) - NE Peru on lower R Ucayali near mouth of R Napo, and W probably to mouth of R Huallaga.



Descriptive notes. Male 8-9 cm, female 7-8 cm; 3-4 g. Male has short straight bill, red tipped black; upperparts shining bronzy-green; chin iridescent blue, underparts iridescent green, variably tinged golden or bluish; tail forked, steel blue. Female upperparts and bill similar to male; underparts white with glittering discs on throat and breast, becoming merely shiny on rest of underparts, undertail-coverts green; tail steel blue. Immature similar to adult female. Male of race *puruensis* has a weak chin spot, less extensive and less defined; *obsoletus* has greener underparts, lacks chin spot.

Habitat. Common in savanna, plantations, town gardens, fields, hedgerows and edges of deciduous woodlands, from sea-level to 500 m. Forages at low to medium heights, 1-6 m.

Food and Feeding. Feeds usually on nectar of flowering garden plants such as *Russelia*, *Salvia*, *Hibiscus*, as well as *Erythrina*, *Heliconia* and coffee bushes. Takes spiders, insects and insect honeydew; insects are caught in the air by hawking. Males establish feeding territories which are aggressively defended against intruders.

Breeding. Aug-Nov. Cup-shaped nest placed on thin branch of small tree or exposed root c. 1 m above ground. Nest materials are fine fibres of plants, leaves and strips of bark. Cobweb is woven in for greater stability, interior is lined with soft material such as downy seeds or seed fibres, outside ornamented with lichen, pieces of leaf, and twigs. Clutch size 2; incubation 14-16 days, by female; chick darkish grey with two dorsal rows of grey down; fledging at 20-22 days. First breeding in second year.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Common throughout range. Readily takes to man-made habitats like plantations and parks. Abundant in forested lowland areas of Trinidad, with density of at least 3-4 pairs/km². Regularly recorded in Henri Pittier National Park (Venezuela), Asa Wright Nature Centre (Trinidad), Kanuku Mts (S Guyana) and around Mana (NW French Guiana).

Bibliography. Bangs & Penard (1918), Berlioz (1932b, 1938, 1965), Butler (1958), de Carvalho (1958), Cotton (1998a), French (1991), Grantsau (1988), Gyldenstolpe (1951), Haverschmidt & Mees (1994), Hayes & Samad (1998), Herklots (1961), Hilty & Brown (1986), Junge & Mees (1958), Meyer de Schauensee & Phelps (1978), Morrison (1962), Parker *et al.* (1982), Riley (1915), Ruschi (1950b, 1957b, 1962f, 1964d, 1981-1982, 1986), Rutgers & Norris (1972), Sick (1993, 1997), Snyder (1966), Stotz, Fitzpatrick *et al.* (1996), Stotz, Lanyon *et al.* (1997), Tostain *et al.* (1992), Walters (1996), Willis (1992), Zimmer (1950d).

91. Blue-tailed Emerald

Chlorostilbon mellisugus

French: Émeraude orvert **German:** Blauschwanz-Smaragdkolibri **Spanish:** Esmeralda Coliazul
Other common names: Golden-crowned Emerald (*auriceps*); Cozumel Emerald (*forficatus*); Fork-tailed/Canivet's Emerald (*canivetii*); Salvin's Emerald (*salvini*); Garden/Allied Emerald (*assimilis*); West Andean Emerald (*melanorhynchus*); Red-billed Emerald (*gibsoni*)

Taxonomy. *Trochilus mellisugus* Linnaeus, 1758, Cayenne.

Forms superspecies with *C. olivaresi*, which may be merely a race of present species (see page 474). Taxonomy highly complex and uncertain: present species has been considered to comprise from two to as many as eight different species by some authors, mainly on basis of differences in bill colour, together with shape of tail and overall coloration. The different forms sometimes raised to full species are: *auriceps*; *forficatus*; *canivetii*; *salvini* (including *osberti*); *assimilis*; *melanorhynchus* (including *pumilus*); and *gibsoni* (including *chrysogaster* and *nitens*). Alternatively, on the basis of bill colour, the five northernmost races have been lumped under *canivetii* as one species, *assimilis* recognized as a separate species, *gibsoni* (including *chrysogaster* and *nitens*) as a third species, and the remaining eight southern races retained as present species; this arrangement has at times been varied by some with the lumping of *assimilis* within the *mellisugus* group, or a transfer of *melanorhynchus* (including *pumilus*) to the *gibsoni* group. However, length of tail and depth of tail-fork appear to decrease consistently from N to S, while red-billed forms appear in both N and S groups; also, the different forms replace each other geographically, with ranges consistently meeting, and until further study produces convincing evidence to the contrary it may be best to treat them all as conspecific. Several of the presently accepted races may be invalid; further study required, especially in zones of possible contact. Proposed race *nanus* of upper and middle Orinoco Valley, at one stage placed in *canivetii* group, may be best considered a synonym of *caribaeus*. Form *napensis* (= *vitticeps*) of Napo Valley (E Ecuador) indistinguishable from *phoeopygus*. Species formerly known as *C. prasinus*, when name *mellisugus* was erroneously thought to apply to *Saucerottia saucerrottei braccata*. Seventeen subspecies currently recognized.

Subspecies and Distribution.

C. m. auriceps (Gould, 1852) - W & C Mexico (S Sinaloa and SW Durango to Guerrero and Oaxaca).
C. m. forficatus Ridgway, 1885 - islands of Holbox, Mujeres and Cozumel, off coast of Yucatán.
C. m. canivetii (Lesson, 1832) - SE Mexico (S Tamaulipas to Yucatán), Belize, N Guatemala and Bay Is (Honduras).
C. m. osberti Gould, 1860 - SE Mexico (extreme SE Chiapas), W & C Guatemala and El Salvador to Honduras and Nicaragua.
C. m. salvini Cabanis & Heine, 1860 - Costa Rica, in highlands of Pacific coast (except regions occupied by next race).
C. m. assimilis Lawrence, 1861 - SW Costa Rica (Térraba Valley and Dota Mts) and arid Pacific coast of Panama (including Pearl Is).
C. m. pumilus Gould, 1872 - arid and semi-arid tropical and subtropical zones of W Colombia and W Ecuador.
C. m. melanorhynchus Gould, 1860 - upper subtropical W Colombia into temperate zone in W & C Andes of Ecuador.

C. m. gibsoni (Fraser, 1840) - upper Magdalena Valley (C Colombia).

C. m. chrysogaster (Bourcier, 1843) - N Colombia from Cartagena to Santa Marta.

C. m. nitens Lawrence, 1861 - NE Colombia and NW Venezuela (W & N of Andes of Mérida).

C. m. caribaeus Lawrence, 1871 - islands of Curaçao, Aruba, Bonaire, Trinidad and Margarita, and NE Venezuela.

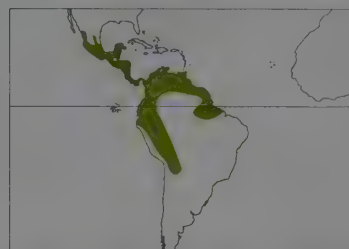
C. m. duidae Zimmer & Phelps, 1952 - Mt Duida (S Venezuela).

C. m. subfurcatus Berlepsch, 1887 - E & S Venezuela, Guyana and the Rio Branco region of NW Brazil.

C. m. mellisugus (Linnaeus, 1758) - Surinam, French Guiana, lower Amazon Valley of Brazil.

C. m. phoeopygus (Tschudi, 1844) - upper Amazon and its eastern tributaries in Colombia, Ecuador, Peru and Bolivia.

C. m. peruanus Gould, 1861 - Peru and E Bolivia.



Descriptive notes. Male 7.5-8.5 cm, female 6.5-7.5 cm; 3-3.5 g. Male has short, straight bill, colour varying with race; forehead and crown iridescent golden green, upperparts shining bronzy-green; underparts glittering emerald green, breast more iridescent than the rest of underparts; tail steel blue, extent of fork varying with race. Female has bill black; bronzy-green on forehead and crown, blackish band across ear-coverts bordered above by pale grey spot behind the eye, rest of upperparts metallic grass green; underparts pale grey; tail mainly blue-black, tipped with whitish-grey. Immature resembles adult female. Races differ mainly in colour of bill, length of tail, depth of tail fork, and overall coloration: varying amounts of red on bill within two groups, northernmost five races and southern *gibsoni*, *chrysogaster* and *nitens*, all other races with totally black bill; length of tail and depth of tail-fork appear to decrease consistently from N to S, being greatest in northern *auriceps* and *forficatus* and shortest in *mellisugus* group; overall coloration ranges from yellowish-orange (*duidae*, *auriceps*) to various shades of green, with more or less marked bluish throat patch; females of some races show more white in tail, and some (e.g. *auriceps*, *canivetii*) have partially red bill.

Habitat. From tropical to temperate zone, mainly between 1000 and 2600 m, but locally to sea-level and recorded up to 3050 m in Loja (S Ecuador). Common in xerophytic habitats like savanna, *cerrado*, cultivated areas, plantations, town gardens, fields, hedgerows and edges of deciduous woodlands. Forages from low to medium heights, c. 1-6 m, occasionally in canopy when orange trees are in flower.

Food and Feeding. Usually feeds low down on nectar of flowering *Hibiscus* and *Cannaceae*, sometimes taking nectar by piercing the petals of *Laminaceae*; further food plants are *Opuntia wentiana*, *Odontoglossum biconiense*, *Epidendrum brassavolae*, *Tamarindus indica*, *Beureria succulenta*, *Acacia tortuosa*, *Cordia sebestena*, *Hibiscus rosa-sinensis*, *Poinciana regia*, *Leonotis nepetifolia* and *Bougainvillea spectabilis*. Takes honeydew from *Diaspididae* found in *bracaatinga* trees (*Mimosa bracaatinga*). Insects are caught in the air by hawking. Trap-liner.

Breeding. Jan-Jun in W and C Andes. Cup-shaped nest is placed in dense, low, second growth woodland c. 0.8 m above ground, fixed on a sloping branch. The lining is of downy plant material. Clutch size 2; incubation 13-14 days, by female; chick darkish grey with two dorsal rows of dark down; fledging at c. 20 days. First breeding in second year.

Movements. Sedentary, seasonal altitudinal dispersal after breeding.

Status and Conservation. Not globally threatened. CITES II. Readily accepts man-made habitat. Generally common throughout much of its extensive range, e.g. in upper Amazonia. The most abundant and widespread hummingbird in Honduras. Race *forficatus* sometimes considered full species, and then classified as restricted-range species: present in Cozumel Island EBA.

Bibliography. Arizmendi & Ornelas (1990), Belcher & Smoother (1936), Berg (1994), Binford (1989), Blake (1953), Bloch *et al.* (1991), Bond (1936), Bond & Meyer de Schauensee (1943), del Campo (1963), Cotton (1998a), Craigie (1928), Davis (1960), Des Granges & Grant (1980), Echeverri (1986), Egg (1969), Eisenmann (1955), Elgar (1980), Feinsinger (1976, 1980), Feinsinger & Colwell (1978), French (1991), Fjeldsá & Krabbe (1990), Fogden (1993), Friedmann (1948), Friedmann *et al.* (1950), Grantsau (1988), Griscom (1932a), Gyldenstolpe (1945a, 1945b), Hartert (1922), Haverschmidt & Mees (1994), Hilty (1985), Hilty & Brown (1986), Howell (1993a), Howell & Webb (1995a), Hummelinck (1957), Johnsgard (1997), Land (1970), Lowery & Dalquest (1951), Lynch (1992), Meyer de Schauensee (1964), Meyer de Schauensee & Phelps (1978), Monroe (1968), Oberholser (1902), Olivares (1969), Olrog (1963c), Parkes (1970), Paynter (1955), Phelps & Phelps (1958), Pinto (1978), Pople *et al.* (1997), Rand & T aylor (1954), Ridgely & Gwynne (1989), Ridgway (1911), Rowley (1962, 1966), Ruschi (1960, 1981-1982, 1982a, 1986), Russell (1964), Schaldach (1963), Schemske (1980), Seutin *et al.* (1997), Sick (1993, 1997), Slud (1964), Smith & Paynter (1963), Snow & Snow (1980), Snyder (1966), Stattersfield *et al.* (1998), Steinbacher (1952), Stiles (1980, 1996), Stiles & Skutch (1989), Stotz *et al.* (1996), Sutton (1898), Thomas (1994), Tiebout (1991a, 1991b, 1993, 1996), Todd (1942), Tostain *et al.* (1992), Underwood (1896), Voous (1983), Wagner (1957b), Wetmore (1939, 1968a), Williams & Tobias (1994), Wolf (1964), Zimmer (1950e).



92. Chiribiquete Emerald

Chlorostilbon olivaresi

French: Émeraude d'Olivares

Spanish: Esmeralda del Chiribiquete

German: Chiribiquete-Smaragdkolibri

Taxonomy. *Chlorostilbon olivaresi* Stiles, 1996, Sierra de Chiribiquete, south-east Colombia. Forms superspecies with *C. mellisugus*, and may be conspecific (see page 474). Monotypic.

Distribution. Sierra de Chiribiquete, in Guaviare and Caquetá (SE Colombia).



Descriptive notes. 8.5-9 cm; male 3-8 g, female 3-6 g. Much larger and longer-billed than *C. mellisugus*. Male has upperparts metallic green, sides of head and neck with strong golden green reflections in fresh plumage; a small greyish-white postocular spot; uppertail-coverts more bluish-green, tail dark steel blue, with shallow fork; throat and upper breast glittering blue-green, passing to bright metallic green on belly and vent. Female metallic bronze-green above, pale grey below; a white postocular stripe above dusky facial area and auriculars; most of tail bluish-green, the lateral rectrices with grey bases, dark blue

subterminal band, white tips. Upper mandible of male black, lower red with black tip; lower mandible of female black, tinged red at base; feet black. Immature resembles adult female but duller, more bronzy above and duller, darker grey below; tail of young male mostly blue-black, outer tail feather tipped dull grey.

Habitat. Open scrub and savanna-like vegetation on flat mesas of middle and upper regions of the Sierra de Chiribiquete; some penetration of adjacent forests where soil is deeper, but not of the taller forests of the surrounding lowlands.

Food and Feeding. Visits scattered flowers of *Decagonocarpus cornutus* in open areas, also blooms of other shrubs or small trees in adjacent wooded areas; not known to defend feeding territories. Sallies to capture small flying insects, mostly at gaps in the vegetation, and gleans tiny insects (including thrips) from foliage and flowers of *Bonnetia* shrubs.

Breeding. Probable season Dec-May, during dry season. Nest undescribed; no further information.

Movements. Sedentary so far as known.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; occurs in Sierra de Chiribiquete Secondary Area. The commonest hummingbird in its unusual, insular habitat, most of which is (nominally) protected in Chiribiquete National Park; since the habitat is unavailable to agriculture or other destructive uses there would appear to be no imminent threat to the species.

Bibliography. Díaz, Stiles & Tellería (1996), Stattersfield *et al.* (1998), Stiles (1996), Stiles *et al.* (1995).

93. Glittering-bellied Emerald

Chlorostilbon aureoventris

French: Émeraude splendide

Spanish: Esmeralda Ventridorada

German: Goldbauch-Smaragdkolibri

Other common names: Pucheran's Emerald (*pucherani*)

Taxonomy. *Ornismya aureo-ventris* d'Orbigny and Lafresnaye, 1838, Rio de Janeiro.

Name "*C. lucidus*", sometimes used for present species, is probably unidentifiable, but, if a synonym, must be regarded as a forgotten name. Race *pucherani* has been considered by some to be approaching the species threshold. Race *igneus* doubtfully separable from nominate. "*H. pyropygia*" is probably a hybrid of present species and *Hylocharis cyanus*. Four subspecies currently recognized.

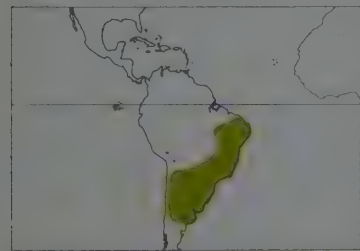
Subspecies and Distribution.

C. a. pucherani (Bourcier & Mulsant, 1848) - E Brazil (Maranhão and Ceará S to Paraná).

C. a. aureoventris (d'Orbigny & Lafresnaye, 1838) - Bolivia, Paraguay and WC Brazil (Mato Grosso).

C. a. igneus Gould, 1861 - NW Argentina (Jujuy and Chaco S to Mendoza and San Luis).

C. a. berlepschi Pinto, 1938 - S Brazil (Rio Grande do Sul) and Uruguay to NE Argentina (Misiones, Entre Rios, Corrientes, Buenos Aires).



Descriptive notes. Male 9.5-10.5 cm, female 7.5-8.5 cm; 3.5-4.5 g. Male has short, straight bill, upper and lower mandibles red, tipped black; crown and forehead dull bronzy-green, upperparts slightly gold-green, uppertail-coverts bronzy green; belly iridescent bronze to bronzy-green, changing to blue-green on throat and upper breast, underparts in general more iridescent than upperparts; tail slightly forked, dark steel blue. Female has bill like male but the black extends to the middle of the bill; forehead, crown and upperparts slightly golden green, greyish-white streak behind the eye; uppertail-coverts grass green; underparts whit-

ish changing to pale brownish-grey on breast and belly; tail slightly forked, rectrices basally green and distally blue, outer four rectrices all steel blue with pale grey V-shaped tips. Immature resembles adult female. Race *berlepschi* differs from nominate in colour of upperparts and underparts (purer green and not gold-green); *igneus* has belly liberally sprinkled with glittering orange-gold; *pucherani* slightly smaller than nominate.

Habitat. Widespread in semi-arid to moderately humid scrub, savanna, grassland, and forest margin habitats in tropical and subtropical zones of the Amazon area to foot of Bolivian Andes; frequent in parks and gardens, from sea-level to 3500 m, commonest at 500-2500 m. Forages at 4-12 m above ground.

Food and Feeding. Feeds on nectar of flowering *Tabebuia*, *Eucalyptus* and *Jacaranda acutifolia* by piercing the petal bases; also on fruits of *Ficus diabolica*. Its preferred flowers are *Lantana*

camara, *Duranta arborea*, *Citrus sinensis*, *Abutilon striatus* and *Eucalyptus robusta*. Feeds by trap-lining. Takes insect honeydew of Coccidae at *Mimosa bruceana*. Insects are caught in the air by hawking.

Breeding. Aug-Nov. Cup-shaped nest placed on thin branch of small tree or exposed root c. 1 m above ground; nest materials are fine plant fibres, pieces of leaf and strips of bark; cobweb is woven in for greater stability; interior lined with soft material such as downy seeds or seed fibres of *Typha domingensis*, Gramineae, Bromeliaceae, *Chorisia* and *Asclepias curassavica*; outside decorated with lichen, pieces of leaf, cortex and twigs, camouflaging the nest. Clutch size 2; incubation c. 14 days, by female; chick darkish grey with two dorsal rows of darkish down; fledging at 20-22 days. First breeding in second year.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Common throughout much of its extensive range. Readily accepts man-made habitats such as gardens, parks and plantations. Within its range in Argentina, is the most commonly seen hummingbird species. Occurs in a number of protected areas throughout range, such as Serra dos Órgãos and Chapada dos Guimarães National Parks (Brazil) and Costanera Sur Ecological Reserve (Argentina).

Bibliography. Belton (1984, 1994), Berlioz (1938, 1949b), Bond & Meyer de Schauensee (1943), Brooks *et al.* (1993), Canevari *et al.* (1991), Contreras (1987), Contreras *et al.* (1990), Dubs (1992), Eisenraut (1935), Fjeldså & Krabbe (1990), Fraga (1984a), Grantsau (1988), Hayes (1995), Hellmayr (1929), Hünig (1999), Klimaitis & Moschione (1987), Kühme (1987), Lowen, Bartrina, Clay & Tobias (1996), Marelli (1938), Narosky & di Giacomo (1993), Navas (1982), Norez *et al.* (1983), Oniki (1996), Oniki & Antunes (1998), de la Peña (1994, 1995), Pereyra (1931), Pinto (1978), Reichholf & Reichholf (1973), do Rosário (1996), Ruschi (1960, 1973d, 1981-1982, 1986), Rutgers & Norris (1972), Saibene *et al.* (1996), Short (1975), Sick (1993, 1997), Stotz *et al.* (1996), Tobias *et al.* (1993), Todd (1938, 1942), Vigil (1973), Wetmore (1926).

94. Cuban Emerald

Chlorostilbon ricordii

French: Émeraude de Ricord

German: Kubasmaragdkolibri

Spanish: Esmeralda Zunzún

Taxonomy. *Ornismya Ricordii* Gervais, 1835, Santiago, Cuba.

Forms a superspecies with *C. swainsonii* and *C. maugaeus*, and these three formerly separated in genus *Riccordia*. In past, considered to include Braze's Emerald (*C. brazei*) as an extinct race, but this form now considered most likely a separate species (see page 533). Monotypic.

Distribution. Cuba (including Cayo Coco, Cayo Largo and nearby cays) and I of Pines, and Bahamas (Grand Bahama, Great Abaco, Andros, Green Cay); casual in rest of Bahamas.



Descriptive notes. Male 10.5-11.5 cm, female 9.5-10.5 cm; 3-4.5 g. Male has slightly decurved, short bill, upper mandible dull black, lower red, tipped black; forehead dull brownish-green, small postocular spot greyish-white, upperparts dark shining green, tinged with bronze, darker and duller on crown; underparts iridescent metallic green, sometimes with a few small spots or greyish streaks on the lateral feathers; undertail-coverts white, sometimes with greyish streaks; tail deeply forked, the four central rectrices dark metallic bronze or greenish-bronze, next pair similar but with inner webs dark brown. Female has upperparts similar to male, longer postocular spot; underparts brownish-grey, sides from neck to flank metallic green, undertail-covert tufts white; tail less forked than male.

Habitat. Occupies a variety of lowland habitats up to 200 m, humid and arid open forest. On Grand Bahama, common in bushy undergrowth of open pine woods, and coastal scrub forest, gardens, parks and plantations. Forages at low to medium height, 1-6 m.

Food and Feeding. Nectar of flowering shrubs and trees, including *Barleria cristata* and *Tabebuia rosae*. Insects are caught in the air by hawking, and occasionally gleaned from spider webs.

Breeding. All year round. Gregarious nesting recorded on Cuba, with 6 nests located, averaging c. 30 cm apart, in cactus-like *Euphorbia nivulia*; no aggression apparent. Cup-shaped nest is loosely woven, composed of moss and silky plant fibres, held together with long trailing tendrils of bark and spider web on outside wall, often flecked with pieces of bark and lichens; nest often found in forks of young branches of coffee and vines 1-3 m above ground; old nest-sites regularly used again. Clutch size 2; incubation 15-16 days, by female; chick dusky coloured with two dorsal rows of buffy white down; fledging period 19-22 days. First breeding in second year.

Movements. Sedentary, some local altitudinal dispersal. Vagrant to Florida, USA.

Status and Conservation. Not globally threatened. CITES II. Readily inhabits man-made habitat. Generally common throughout much of its extensive range. On Andros (Bahamas), density of at least 3-4 pairs/km² recorded.

Bibliography. Alayón (1980), Allen (1961), Anon. (1998a), Barbour (1943), Behnke-Pedersen (1972), Bond (1956a, 1985), Brudenell-Bruce (1975), Buden (1987b), Chapman (1902), DeBenedictis (1991), Emlen (1977), García & Rojas (1997), Gundlach (1876), Hernández & Tadeo (1997), Johnsgard (1997), Kale (1977), Lack (1976), Paterson (1972a), Raffaele *et al.* (1998), Regalado (1998), Ridgway (1911), Robertson & Woolfenden (1992), Rutgers & Norris (1972), Stimson (1944), Stotz *et al.* (1996), Terres (1982), Todd (1942), Tyrrell & Tyrrell (1990), Vaune (1957).

95. Hispaniolan Emerald

Chlorostilbon swainsonii

French: Émeraude d'Hispaniola

Spanish: Esmeralda de la Española

German: Hispaniolansmaragdkolibri

Taxonomy. *Ornismya Swainsonii* Lesson, 1829, Brazil; error = Hispaniola.

Forms a superspecies with *C. ricordii* and *C. maugaeus*, and these three formerly separated in genus *Riccordia*. Monotypic.

Distribution. Hispaniola; erroneously recorded from Gonâve.

Descriptive notes. Male 9.5-10.5 cm, female 8.5-9.5 cm; 2.5-5 g. Male has maxilla black, mandible red, distal third slightly decurved; forehead, crown, and cheeks dull dark brown, rest of upperparts



and flanks dark green with some bronze, uppertail-coverts dark green; underparts darker green than upperparts, throat iridescent green with large blackish patch on centre of breast, undertail-coverts dark green; tail deeply forked, dark brown. Female has bill more decurved than male; forehead, crown and cheeks dull dark brown, rest of upperparts and flanks dark green tinged with bronze, uppertail-coverts dark green; underparts grey, darker on belly and undertail-coverts; outer rectrix basally greyish, with a broad dark brown subterminal band, tipped white, next rectrix basally dark grass green, shading into black,

the remaining rectrices green. Immature resembles adult female.

Habitat. Dense montane rainforest, forest edges and scrub, at 500–2500 m, occasionally to sea-level. Forages in low to high strata at 3–18 m.

Food and Feeding. Feeds on nectar of flowering *Heliconia bihai*, *Rhytidophyllum auriculatum*, *Caesalpinia pulcherrima*, *Aechmea* and *Hibiscus*. Trap-liner; hawks for insects in the air.

Breeding. Feb–Jun, but with irregular nesting throughout the year. Large cup-shaped nest of moss and fern fibres, externally decorated with lichen, built in shrubs 0.5–1 m above ground. Clutch size 2; incubation 15–16 days, by female; chick dark grey with two rows of darkish dorsal down; fledging at 20–22 days. First breeding in second year.

Movements. Sedentary, with occasional altitudinal wandering.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Hispaniola EBA. Most of its very small range is under threat of deforestation, especially Haitian part of Hispaniola. Readily accepts man-made habitats as long as patches of forest remain.

Bibliography. Allen (1961), Anon. (1998a), Behnke-Pedersen (1972), Bond (1928a, 1956a, 1985), Curzon (1998), Dod (1987, 1992), Lack (1976), Raffaele *et al.* (1998), Ridgway (1911), Rimmer *et al.* (1998), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Todd (1942), Tyrrell & Tyrrell (1990), Wetmore & Swales (1931).

96. Puerto Rican Emerald

Chlorostilbon maugaeus

French: Émeraude de Porto Rico

Spanish: Esmeralda Portorriqueña

German: Puerto-Rico-Smaragd Kolibri

Other common names: Antillean Emerald

Taxonomy. *Trochilus Maugaeus* Audebert and Vieillot, 1801, Puerto Rico.

Forms a superspecies with *C. ricardii* and *C. swainsonii*, and these three formerly separated in genus *Riccordia*. Monotypic.

Distribution. Puerto Rico.



Descriptive notes. Male 8.5–9.5 cm, female 7.5–8.5 cm; 3.4–3.8 g. Male has short straight bill, upper mandible dull black, lower red, tipped black; forehead and crown iridescent green, dark shining metallic green upperparts and uppertail-coverts; throat iridescent bluish-green, rest of underparts and undertail-coverts shining green; tail forked, shining steely blue. Female has bill black; forehead and crown dull dark green; upperparts and uppertail-coverts shining grass green; throat and breast are light grey becoming darker on belly; tail less forked, outer rectrices basally pale white, becoming brown in centre and tipped with a large white

spot, second outermost rectrices shining greenish-white at base changing to steel blue, tipped with white spot, the next innermost two are green from base to centre, rest of feather dull brown, the inner rectrices are shining green. Immature resembles adult female.

Habitat. Coastal mangroves to forested mountain summits. Open forest, woodland and coffee plantations, from sea-level to 800 m. Forages in low to medium strata, c. 1–6 m.

Food and Feeding. Feeds on nectar of a wide spectrum of flowers, including *Hohenbergia portoricensis*, *Vriesea sintenisii*, *Dilomilis montana*, *Epidendrum* sp., *Hedychium coronarium*, *Renealmia antillarum*, *Justicia martinsoniana*, *Ruellia coccinea*, *Sanchezia nobilis*, *Thumbbergia erecta*, *Spathodea campanulata*, *Tabebuia haemantha*, *T. rigida*, *T. schumanniana*, *Clusia krugiana*, *C. minor*, *Erythrina berterouana*, *Neorudolphia volubilis* and *Sabinea punicea*. Trap-liner. Arthropod diet includes flies, Homoptera, Hymenoptera and small spiders, gleaned from branches and leaves of trees.

Breeding. Feb–May, but irregular nesting all year round. The nest, a compact structure in the form of a small cup, is composed of dry plant fibres, such as tree fern scales, lined with wild cotton and other soft plant material, externally decorated with lichen. It is generally built in either low or medium-sized plants and trees. Clutch size 2; incubation 14–16 days, by female; chick darkish grey with two rows of dark down on the upperside; fledging at 20–22 days. First breeding in second year.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Puerto Rico and the Virgin Islands EBA. Readily accepts man-made habitats like plantations, gardens and parks. Generally common throughout Puerto Rico.

Bibliography. Allen (1961), Anon. (1998a), Behnke-Pedersen (1972), Biaggi (1983), Bond (1956a, 1985), Kodric-Brown *et al.* (1984), Lack (1976), Orelas (1994), Otero (1998), Raffaele (1989), Raffaele *et al.* (1998), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Todd (1942), Tyrrell & Tyrrell (1990), Wetmore (1916, 1927).

97. Coppery Emerald

Chlorostilbon russatus

French: Émeraude cuivrée

Spanish: Esmeralda Bronceada

German: Bronzeschwanz-Smaragd Kolibri

Taxonomy. *Panychlora russata* Salvin and Godman, 1881, Manaua, San Sebastián and San José, Santa Marta, Colombia.

Monotypic.

Distribution. NE Colombia (lower Magdalena Valley and Santa Marta region) and NW Venezuela.



Descriptive notes. Male 8–8.5 cm, female 7–7.5 cm; 3.2–3.6 g. A very distinctive species, readily distinguished from its congeners by rich coppery gloss of the tail-coverts and wing-coverts in both sexes. Male has short, straight, black bill; forehead, crown and upperparts shining golden green, uppertail-coverts coppery green; underparts glittering golden green; tail slightly forked, golden coppery. Female has bill like male; forehead, crown and uppertail-coverts coppery green; underparts smokey grey with some green on flanks; tail slightly forked, greenish-coppery, all but central tail feathers with coppery purple subterminal band, tipped pale. Immature resembles adult female but with buffy fringes on head feathers.

Habitat. Scrub, forest edge and cultivated areas such as plantations and farms; from sea-level to 2600 m, commonest at 500–1700 m. Forages at low to moderate heights, around 4–12 m.

Food and Feeding. Feeds on nectar of Leguminosaceae, Rubiaceae, Heliconiaceae and Gesneriaceae. Trap-liner. Insects are caught in the air by hawking, occasionally gleaned from plant surfaces.

Breeding. May–Jun. Cup-shaped nest is placed around 0.8 m above ground, fixed on a sloping branch; lining is of downy plant material. Clutch size 2; incubation 15–16 days, by female; chick darkish grey with two dorsal rows of dark down; fledging at c. 20 days. First breeding in second year.

Movements. Sedentary, with seasonal local altitudinal dispersal, especially after reproduction.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Santa Marta Mountains EBA and Colombian East Andes EBA. A species with patchy distribution, generally uncommon to locally common. Quickly takes to man-made habitats like plantations and parks with scattered trees.

Bibliography. Avelledo & Pons (1952), Berlepsch (1888), Boucard (1892b), Chapman (1917), Fjeldså & Krabbe (1990), Hilty & Brown (1986), Meyer de Schauensee (1949, 1964, 1982), Meyer de Schauensee & Phelps (1978), Oberholser (1902), Olivares (1969), Olrog (1968), Phelps & Phelps (1958), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Todd (1942), Todd & Carriker (1922).

98. Narrow-tailed Emerald

Chlorostilbon stenurus

French: Émeraude à queue étroite

Spanish: Esmeralda Colifina

German: Schmalschwanz-Smaragd Kolibri

Taxonomy. *Panychlora stenura* Cabanis and Heine, 1860, Mérida.

Possibly forms a superspecies with *C. alice* and *C. poortmani*. Race *ignotus* sometimes considered synonymous with *C. alice*, or treated as a hybrid. Birds of Colombia and Ecuador have been separated as race *acuticaudus*, but doubtfully valid. Two subspecies recognized.

Subspecies and Distribution.

C. s. ignotus Todd, 1942 - NW Venezuela, from coastal range S to highlands of extreme SE Lara. *C. s. stenurus* (Cabanis & Heine, 1860) - NW Venezuela (Trujillo, Mérida, Táchira) and NE Colombia (Norte de Santander possibly S to W Meta); NE Ecuador (Baeza).



Descriptive notes. Male 8.5–9 cm, female 7.5–8 cm; 3.2–3.6 g. Male has short, straight, black bill; forehead and crown shining green, upperparts including uppertail-coverts shining grass green; underparts and flanks iridescent green; tail forked, dark green, outer two rectrices very small, stiletto-like, remainder normally shaped. Female has bill slightly decurved; small white streak above and behind eye, and small brown bristles at basal part of bill; crown dull dark green with some bronze, the remaining upperparts and uppertail-coverts dark green; brownish chin, underparts pale white, throat lighter than belly; tail slightly

forked, outer two rectrices grey at the base, becoming dark blue with a broad white V-shaped tip, the next innermost are metallic green at the base, shading into brown with a small white V-shaped tip, central rectrices metallic bluish-green. Immature resembles adult female. Race *ignotus* is smaller, more yellowish-green above, and has duller, darker green tail.

Habitat. Humid forest, low scrub, second growth, at 1000–3000 m. Forages in low to mid-strata at 0.6–4 m.

Food and Feeding. Feeds in rather open areas on nectar of scattered low flowers with horizontal or upright corollas, like Ericaceae, Gesneriaceae, Rubiaceae, Heliconiaceae, or *Inga*. Trap-liner. Insects are caught in the air by hawking.

Breeding. Sept–Nov. Nest is cup-shaped, built of moss and decorated externally with lichen; in shrubs and lower parts of trees, 1–2 m above the ground. Clutch size 2; incubation 15–16 days, by female; chick darkish grey with two dorsal rows of dark down; fledging at c. 20 days. First breeding in second year.

Movements. Sedentary, with local altitudinal dispersal.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Cordillera de Mérida EBA and Colombian East Andes EBA. Common throughout range: Readily accepts man-made habitats. Particularly abundant above city of Mérida.

Bibliography. Behnke-Pedersen (1972), Chapman (1926), Fjeldså & Krabbe (1990), Hilty & Brown (1986), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Oberholser (1902), Olrog (1968), Phelps & Phelps (1958), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Todd (1942).

99. Green-tailed Emerald

Chlorostilbon alice

French: Émeraude alicé

German: Grünschwanz-Smaragd Kolibri

Spanish: Esmeralda Coliverde

Taxonomy. *Trochilus Alice* Bourcier and Mulsant, 1848, Caracas.

Possibly forms a superspecies with *C. stenurus* and *C. poortmani*. *C. stenurus ignotus* has been considered synonymous with present species. Probably includes *C. micans*, with all of plumage rich reddish-golden, known only from type specimen of unknown origin. "*Ptychoptera iolaima*",

known from a specimen taken at Ypanema, São Paulo (Brazil), is probably a hybrid between present species and *C. poortmani*. Monotypic.

Distribution. Mountainous regions of N Venezuela, from Falcón (Sierra de San Luis) S to Lara and Trujillo, and E to Sucre and N Monagas.



Descriptive notes. Male 7.5-8.5 cm, female 6.5-7.5 cm; 3-4 g. Male has short, straight, black bill; forehead and crown shining dark green, upperparts, wing-coverts and tail-coverts bronzy-green; underparts including undertail-coverts grass green; tail slightly forked, glittery bronzy-green. Female similar to male; underparts pale greyish, undertail-coverts dark grey; tail slightly forked, central rectrices green, rest green at base, becoming subterminally black, tipped greyish. Immature resembles adult female with buffy fringes on head feathers.

Habitat. Edges of rainforest and cloudforest;

also second growth and plantations; rarely seen in dense forest. Prefers wide and open areas and roadsides, at 700-1800 m. Forages in low to mid-strata at 1-6 m.

Food and Feeding. Feeds on nectar of various flowering shrubs and trees, including Leguminosaceae, Rubiaceae, Gesneriaceae and Ericaceae. Males occupy feeding territories at rich nectar sources. Trap-liner. Insects are caught in the air by hawking.

Breeding. Jan-Mar. Cup-shaped nest is built in shrubs and low trees, c. 1 m above ground, saddled on thin branches. Nest materials are fine plant fibres, pieces of leaves and strips of bark, interior lined with soft downy seeds or seed fibres, externally decorated with pieces of leaves and twigs. Clutch size 2; incubation 14 days, by female; chick darkish grey with two dorsal rows of darkish down; fledging at 20-22 days. First breeding in second year.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Caripe-Paria Region EBA, Cordillera de la Costa Central EBA and Cordillera de Mérida EBA. Locally common. Readily accepts man-made habitats such as plantations, parks, gardens, etc. with scattered stands of shrubs and trees.

Bibliography. Behnke-Pedersen (1972), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Olrog (1968), Phelps & Phelps (1958), Renjifo *et al.* (1997), Rodner (1995), Schäfer & Phelps (1954), Stattersfield *et al.* (1998), Stoltz *et al.* (1996), Todd (1942), Wetmore (1939).

100. Short-tailed Emerald

Chlorostilbon poortmani

French: Émeraude à queue courte

Spanish: Esmeralda Colicorta

German: Kurzschwanz-Smaragdkolibri

Other common names: Berlepsch's Emerald ("inexpectatus")

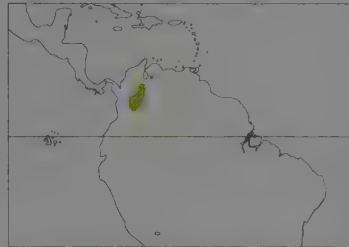
Taxonomy. *Ornismya poortmani* Bourcier, 1843, Colombia.

Possibly forms a superspecies with *C. stenurus* and *C. alice*. Race *euchloris* has sometimes been considered a separate species, due mainly to suggestion of possible overlap in range, but poorly known. Forms "*inexpectatus*" and "*auratus*", known by single specimens from "Bogotá" and "Peru" respectively, are apparently aberrant individuals of present species. "*Ptichoptera iolaima*", known from a specimen taken at Ypanema, São Paulo (Brazil), is probably a hybrid between present species and *C. alice*. Two subspecies recognized.

Subspecies and Distribution.

C. p. euchloris (Reichenbach, 1854) - C Colombia (W slope of E Andes S to Huila, and E slope in Santander).

C. p. poortmani (Bourcier, 1843) - E Colombia (E slope of E Andes, from Boyacá S to W Meta) and NW Venezuela (Mérida and Táchira).



Descriptive notes. Male 7.5-8.5 cm, female 6.5-7.5 cm; 3-4 g. Male has short, straight, black bill; forehead iridescent green, crown bronzy-green, all upperparts, wing-coverts and tail-coverts are bronzy-green; underparts, including undertail-coverts, are brilliant glittery green; tail forked, short, iridescent bronzy-green. Female has bill like male; forehead dull green, crown dull bronzy-green; upperparts similarly coloured to those of male, but far less brilliant; underparts grey; tail forked, short, central tail feathers green, others basally dull turquoise shading to dark blue, tipped pale grey. Immature resembles adult female but with

buffy fringes on head feathers. Race *euchloris* very similar but slightly larger, with slightly more golden tinge to crown and underparts.

Habitat. Humid forest, forest edge, open woodland, second growth, plantations, usually along stream, at 100-2400 m.

Food and Feeding. Visits non-pendent flowers such as *Elleanthus*, *Guzmania* and *Phaseolus*. Mostly a trap-liner at scattered low flowers 0.6-4 m above ground in rather open areas. In coffee plantations feeds on nectar of flowering *Inga* trees. Insects are caught in the air by hawking.

Breeding. May-Jun. Cup-shaped nest has a thin and soft texture created by cotton or fibrous fluff; outside decorated with fragments of leaves, branches, fine roots, moss and scales of Cycadaceae. Clutch size 2; incubation 15-16 days, by female; chick darkish grey with two dorsal rows of dark down; fledging period 20-22 days. First breeding in second year.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Cordillera de Mérida EBA and Colombian East Andes EBA. Generally common throughout much of its extensive range. Readily accepts man-made habitats.

Bibliography. Fjeldså & Krabbe (1990), Hilty & Brown (1986), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Olivares (1969), Olrog (1968), Phelps & Phelps (1958), Ruschi (1949b), Salaman & Mazariegos (1998a), Snow & Snow (1980), Stattersfield *et al.* (1998), Stoltz *et al.* (1996), Todd (1942).



Genus *PANTERPE* Cabanis & Heine, 1860

101. Fiery-throated Hummingbird

Panterpe insignis

French: Colibri insigne **German:** Feuerkehlkolibri **Spanish:** Colibrí Insigne
Other common names: Irazu Hummingbird

Taxonomy. *Panterpe insignis* Cabanis and Heine, 1860, "San José" (probably Volcán Irazú), Costa Rica.

Relationships uncertain. Two subspecies recognized.

Subspecies and Distribution.

P. i. eisenmanni Stiles, 1985 - N Costa Rica (Cordillera de Guanacaste).

P. i. insignis Cabanis & Heine, 1860 - NC Costa Rica (Cordillera de Tilarán) S to extreme W Panama.



Descriptive notes. 10.5-11 cm; male 5.9-6.2 g, female 4.9-5.2 g. Sexes alike. Bill black except basal part of lower mandible pink, feet dusky grey. Crown glittering royal blue, sides of head and nape black, small white postocular spot; back bright metallic green, shading to bluish-green on uppertail-coverts; tail blue-black; throat golden green laterally, shading to brilliant rosy copper-orange centrally; violet-blue patch on centre of breast; belly and vent bright green to blue-green. Immature has rusty borders to feathers of face and nape. Race *eisenmanni* slightly smaller than nominate with blue-violet of chest extending to belly, black

of nape extending to upper back, uppertail-coverts mostly blue, bill much shorter.

Habitat. Montane forest, cloudforest including elfin forest, timberline shrubbery of sub-*páramo*, clearings and second growth adjacent to forest, highland pastures with many remnant trees. Mostly in canopy inside forest, descending to shrub level at edges and in adjacent clearings. At 2200-3200m in higher mountains; in lower cordilleras of N and NC Costa Rica occurs from 1600-1800 m to summits.

Food and Feeding. Visits a wide variety of flowers of epiphytes (bromeliads, ericads, gesneriads), shrubs and small trees (*Gaiadendron*, *Vaccinium*, *Cestrum*, *Centropogon*, *Fuchsia*), vines (*Tropaeolum*, *Bomarea*), herbs (*Salvia*) and those of *Clusia* trees in cloud and elfin forest. Pierces longer flowers of *Centropogon* and *Fuchsia*, or uses holes made by bumblebees or flowerpiercers (*Diglossa*) to reach nectar. Very aggressive and dominant at flowers, both sexes frequently defending feeding territories outside the breeding season. Frequently hawks small flying insects, less often gleans arthropods from foliage.

Breeding. Aug-Jan in Costa Rica. During breeding males do not lek but defend rich patches of flowers, usually of ericads (*Macleania*, *Cavendishia*) into which they allow females with whom they mate. Nest a bulky cup of treefern scales, plant down and cobweb, heavily decorated on the outside with green moss and bits of lichen, attached to tip of drooping bamboo stem inside forest or dangling root under overhanging bank of road-cut, 2-4 m above ground. Clutch size 2. No further information.

Movements. Following breeding at least part of population moves to lower elevations, down locally to 1400-1600 m, rarely to 700 m.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Costa Rica and Panama Highlands EBA. Species is generally common to abundant over most of range. Large areas of its montane habitats are protected in national parks or forest reserves in Costa Rica and Panama, e.g. Volcán Irazú and Volcán Poás National Parks and Monteverde Biological Reserve (Costa Rica).

Bibliography. Anon. (1998a), Blake (1958), Feinsinger (1980), Fogden (1993), Law & Fogden (1981), Ridgely & Gwynne (1989), Skutch (1967), Slud (1964), Stattersfield *et al.* (1998), Stiles (1983b, 1985a, 1985c), Stiles & Skutch (1989), Stotz *et al.* (1996), Tramer & Simmers (1994), Wetmore (1968a), Wolf (1969, 1976), Wolf & Hainsworth (1972), Wolf & Stiles (1970), Wolf *et al.* (1976).

Genus *ELVIRA* Mulsant *et al.*, 1866

102. White-tailed Emerald

Elvira chionura

French: Colibri elvire **German:** Grüner Elvirakolibri **Spanish:** Esmeralda Elvira

Taxonomy. *Trochilus* (*Thaumantias*?) *chionura* Gould, 1851, David, Chiriquí, Panama.

Genus sometimes merged into *Eupherusa*. Monotypic.

Distribution. Pacific slope from S Costa Rica to C Panama; reaches Caribbean slope locally in Panama.

Descriptive notes. 7.5-8 cm; male 3.3 g, female 3.1 g. Bill nearly straight, black except for pinkish basal half of lower mandible, feet dark grey. Male bronzy-green above, shading to dark copper-bronze on uppertail-coverts and central rectrices; outer 3 rectrices white, tipped black; below mostly glittering green, belly, vent and undertail-coverts white. Female dull white below flecked with green laterally and bronzy-green on flanks; central rectrices bronzy, outer 3 white crossed by diagonal black subterminal band. Immature male duller green below than adult, with greyish-buff feather fringes; immature female greyer below than adult, green lateral spotting duller, more bronzy and



Movements. Not well understood; outside breeding season recorded both above and below breeding areas in Costa Rica.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Costa Rica and Panama Highlands EBA. Locally common in lower part of La Amistad National Park and at Las Cruces Biological Station in Costa Rica; however, deforestation extensive and continuing in at least the lower part of its altitudinal range in both Costa Rica and Panama; its current status requires more thorough documentation.

Bibliography. Anon. (1998a), Blake (1958), Hernández-Baños *et al.* (1995), Renjifo *et al.* (1997), Ridgely & Gwynne (1989), Slud (1964), Stattersfield *et al.* (1998), Stiles (1985c), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968a).

103. Coppery-headed Emerald

Elvira cupreiceps

French: Colibri à tête cuivrée **Spanish:** Esmeralda Capirotada
German: Bronzekopf-Elvirakolibri

Taxonomy. *Eupherusa cupreiceps* Lawrence, 1866, Barranca, Costa Rica.

Genus sometimes merged into *Eupherusa*. Species has occasionally been awarded monospecific genus *Lawrencius*. Population of Cordillera de Guanacaste (N Costa Rica) probably deserves recognition as a separate race. Monotypic.

Distribution. Highlands of N & C Costa Rica: Caribbean slope, reaching Pacific slope in upper parts of N Cordillera de Guanacaste and N Cordillera de Tilarán.



Descriptive notes. 7.5 cm; male 3.4 g, female 3.1 g. Distinctly decurved bill black except for pinkish base of lower mandible. Male has crown, uppertail-coverts and central rectrices copper-bronze, otherwise bronzy-green above, glittering green below, vent and undertail-coverts white, 3 lateral rectrices white, tipped dark grey. Female has crown and back green, underparts dull white speckled laterally with brown, white outer rectrices crossed by a broken blackish band. Male in Cordillera de Guanacaste differs from those in remainder of range in possessing a distinct purple spot in centre of lower breast. Young male has under-

parts dull bronzy-green, crown dull green only slightly tinged with copper; both sexes show cinnamon fringes to feathers on face, nape and rump.

Habitat. Cool, wet highland forests, forest edge, pastures with many remnant forest trees, shaded coffee plantations, old second growth. In forest, male mostly in canopy, female more in understorey; both sexes at all levels along edges and in semi-open, second growth. Breeds mainly at 700-1500 m, lower outside breeding season.

Food and Feeding. Takes nectar from flowers of various trees (*Quararibea*, *Pithecellobium*, *Guarea*, *Clusia*), epiphytes (especially Ericaceae, Gesneriaceae), shrubs (Acanthaceae, *Besleria*) in forest, and of *Inga* trees and *Stachytarpheta* shrubs in and beside coffee plantations and in second growth. Takes arthropods by flycatching, usually sallying from perch, and by gleaning from foliage at all levels.

Breeding. In wet and early dry seasons, Oct-Mar. During breeding season males form leks of 3-6. Nest a neat cup of treefern scales, plant down and spiderweb, heavily decorated with moss and a few bits of lichen, 1-3 m above ground in shrub or fern in forest understorey, at edge, or along trail, stream, etc. Clutch size 2. No further information.

Movements. Makes pronounced altitudinal movements, bulk of population descending to 300-600 m, occasionally lower, following breeding.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Costa Rica and Panama Highlands EBA. Common over most of range, which includes large protected areas in all cordilleras, e.g. Braulio Carrillo, Rincón de la Vieja and Guanacaste National Parks, and Monteverde Biological Reserve.

Bibliography. Anon. (1998a), Feinsinger (1976, 1977, 1980), Fogden (1993), Hernández-Baños *et al.* (1995), Renjifo *et al.* (1997), Ridgway (1911), Slud (1964), Stattersfield *et al.* (1998), Stiles (1985b, 1985c), Stiles & Skutch (1989), Stotz *et al.* (1996).

Genus *EUPHERUSA* Gould, 1857

104. Oaxaca Hummingbird

Eupherusa cyanophrys

French: Colibri d'Oaxaca **German:** Blauscheitkolibri **Spanish:** Colibrí Oaxaqueño

On following pages: 105. White-tailed Hummingbird (*Eupherusa poliocerca*); 106. Stripe-tailed Hummingbird (*Eupherusa eximia*); 107. Black-bellied Hummingbird (*Eupherusa nigriventris*); 108. Pirre Hummingbird (*Goethalsia bella*); 109. Violet-capped Hummingbird (*Goldmania violiceps*); 110. Dusky Hummingbird (*Cyananthus sordidus*); 111. Broad-billed Hummingbird (*Cyananthus latirostris*); 112. Blue-headed Hummingbird (*Cyanophaea bicolor*).

Other common names: Blue-capped Hummingbird

Taxonomy. *Eupherusa cyanophrys* Rowley and Orr, 1964, 11 miles [c. 18 km] south of Juchatengo, south-western Oaxaca, Mexico.

Forms a superspecies with *E. polioerca* and *E. eximia*; sometimes regarded as a race of former, but morphological differences justify status as separate full species. Monotypic.

Distribution. Mountains of S Oaxaca (SC Mexico).



(mainly *Chusquea*), semi-deciduous forest, gallery forest, and cloudforest, at 700-2600 m, commonest below 1800 m. Forages in all strata.

Food and Feeding. Feeds on nectar of flowering *Inga*, *Kohleria*, *Lobelia*, *Malviscus*, *Manettia*, *Psittacanthus* and *Hamelia patens*; subordinate to other hummingbirds, such as *Amazilia*.

Breeding. Sept-Nov. May. Cup-shaped nest, made of moss, lined with plant down, exterior decorated with lichens, two nests incorporated flowers of *Salvia*; placed in forks of small bushes, exposed roots, and small trees, 1-2-6 m above ground. The 6 m record is probably an exception since it was located in a steep road cutting on an exposed pine root. Clutch size 2, incubation by female. No further information.

Movements. Sedentary; some seasonal vertical dispersal to lower and higher elevations.

Status and Conservation. **ENDANGERED.** CITES II. Restricted-range species: present in Sierra Madre del Sur EBA. Locally common but highly restricted in range. Habitat is unprotected and threatened by deforestation. Shortly after its discovery it was realized that species was vulnerable to deforestation resulting from the methods used by local human population to cultivate corn; the preferred slash-and-burn practices cause severe damage to remaining forest areas. Species frequently recorded in the area around Santa Rosa and Río Salado, and between Pluma Hidalgo and La Soledad.

Bibliography. Anon. (1998a), Binford (1989), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Hernández-Baños *et al.* (1995), Howell & Webb (1995a), Johnsgard (1997), Mayr (1971), Roberson & Carratello (1997), Rowley (1966), Rowley & Orr (1964), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Webster (1965), Wege & Long (1995).

105. White-tailed Hummingbird

Eupherusa polioerca

French: Colibri du Guerrero **German:** Weißschwanzkolibri **Spanish:** Colibrí de Guerrero

Taxonomy. *Eupherusa polioerca* Elliot, 1871, Putla, Oaxaca, Mexico.

Forms a superspecies with *E. cyanophrys* and *E. eximia*; sometimes regarded as conspecific with former, but morphological differences justify their separation as two full species. Monotypic.

Distribution. Pacific slope of Guerrero (Sierra Madre del Sur) and W Oaxaca, S Mexico.



Food and Feeding. Feeds on nectar of flowering *Inga*, *Kohleria*, *Lobelia*, *Malviscus*, *Manettia*, *Psittacanthus* and *Hamelia patens*; subordinate to other hummingbirds like *Amazilia*.

Breeding. One nest has been found in Oct, birds in breeding condition in Feb and Apr. No further data available.

Movements. Sedentary; some altitudinal dispersal likely.

Status and Conservation. **ENDANGERED.** CITES II. Restricted-range species: present in Sierra Madre del Sur EBA. Still locally common within its restricted range. Although may accept man-made habitats like coffee plantations to some extent, species is threatened by destruction of its natural habitat by deforestation. Common in the Omiltemi State Ecological Park, which is protected; however, most of range remains unprotected.

Bibliography. Anon. (1998a), Binford (1989), Ceballos-Lascurain (1989), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Friedmann *et al.* (1950), Hartert & Hartert (1894), Hernández-Baños *et al.* (1995), Howell & Webb (1995a), Johnsgard (1997), Knox & Walters (1994), Mayr (1971), Montes de Oca (1875), Navarro (1992), Navarro & Muñoz (1990), Navarro *et al.* (1991), Ornelas (1987), Rowley & Orr (1964), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Wege & Long (1995).

106. Stripe-tailed Hummingbird

Eupherusa eximia

French: Colibri à épaulettes **German:** Streifenschwanzkolibri **Spanish:** Colibrí Colirrayado

Taxonomy. *Ornismya eximia* DeLattre, 1843, Cobán, Guatemala.

Forms a superspecies with *E. cyanophrys* and *E. polioerca*. Three subspecies recognized.

Subspecies and Distribution.

E. e. nelsoni Ridgway, 1910 - E & SE Mexico.

E. e. eximia (DeLattre, 1843) - extreme E Mexico S through highlands to C Nicaragua.

E. e. egregia P. L. Sclater & Salvin, 1868 - highlands of Costa Rica and W Panama.



upperparts. Male of *nelsoni* more yellowish-green below, black tips of outer rectrices more diffuse; *egregia* has black of outer webs of lateral rectrices restricted to narrow border; in latter race these feathers usually wholly white in female.

Habitat. Canopy and borders of cool, wet highland forest, descending to shrub level in gaps, along forest borders, or in adjacent semi-open or second growth vegetation; only nesting female regularly uses heavily shaded forest understory, especially in ravines and near streams. Occurs at 1000-1800 m (Honduras), mostly 800-2000 m (Costa Rica), 1200-2500 m (Panama).

Food and Feeding. Visits flowers of a variety of trees, including *Inga* and *Clusia*, shrubs, especially Acanthaceae and Rubiaceae, also *Besleria* and *Salvia*, and epiphytes, notably Ericaceae and Gesneriaceae. Sometimes pierces long corollas; male in particular often very aggressive and territorial at flowers. Flycatches especially at gaps and edges, and gleans arthropods from foliage and mossy trunks.

Breeding. Late wet into dry season, Sept-Mar or Apr in Costa Rica; Apr-Jun in Oaxaca, Mexico. Nest a neat cup of pale-colored plant down, fine fibres, treefern scales and cobweb, decorated on outside with moss and lichens, usually including bits of a bright red lichen, 1-3 m up in dark forest understory, often near a stream. No further information.

Movements. In Costa Rica and probably Panama often descends to lower elevations, locally down to 250-300 m, during non-breeding season; immediately following breeding, small numbers may also range upslope, to 2500 m or more.

Status and Conservation. Not globally threatened. CITES II. Locally uncommon to common over most of range, where deforestation has not been severe. Regularly recorded in the Mayan ruins of Palenque, Chiapas (Mexico), and at Monteverde Biological Reserve (Costa Rica). In Mexico, populations of race *nelsoni* may be under pressure from habitat destruction, but more information required on current situation.

Bibliography. Anon. (1998a), Binford (1989), Blake (1958), Carroll & Moore (1993), Feinsinger (1976, 1977, 1980), Feinsinger *et al.* (1987), Fogden (1993), Friedmann *et al.* (1950), Howell & Webb (1995a), Howell *et al.* (1992), Johnsgard (1997), Land (1970), Monroe (1968), Paynter (1957), Renjifo *et al.* (1997), Ridgely & Gwynne (1989), Ridgway (1911), Rowley (1984), Russell (1964), Slud (1964), Stiles (1985c), Stiles & Skutch (1989), Stotz *et al.* (1996), Thomas *et al.* (1986), Wetmore (1968a).

107. Black-bellied Hummingbird

Eupherusa nigriventris

French: Colibri à ventre noir **German:** Schwarzbauchkolibri **Spanish:** Colibrí Ventrinegro

Taxonomy. *Eupherusa nigriventris* Lawrence, 1867, Costa Rica.

In past, sometimes segregated in monospecific genus *Callipharus*. Monotypic.

Distribution. Highlands of Caribbean slope from C Costa Rica to W Panama.



Descriptive notes. 7.5-8.5 cm; male 3-7 g, female 3-3 g. Rather short blackish bill, slightly decurved. Bronzy-green above, dusker on central rectrices; male has forecrown, face and underparts velvety black; female grey below flecked laterally with bronze-green; rufous patch on secondaries, smaller and duller in female. Outer 3 rectrices mostly white. Immature male has black of face and underparts replaced by dark sooty bronze; young of both sexes with dusky fringes on feathers of face, crown, nape and rump; dark border of outer web of third rectrix wider and more diffuse.

Habitat. Cool, wet highland forest, forest edge, adjacent semi-open vegetation including shaded pastures and coffee plantations, tall second growth. Mostly at 900-2000 m in Costa Rica, 1300-1800 m in Panama. In forest, male mostly in upper understory and canopy, female in understory; both sexes descend to shrub level along edges and gaps and in second growth.

Food and Feeding. In forest, male visits mostly flowers of trees (*Inga*, *Calliandra*, *Pithecellobium*, *Clusia*) and epiphytes (Ericaceae, *Columnnea*, *Norantea*, *Elleanthus*), female more at flowers of shrubs like *Besleria*, *Cephaelis*, or *Witheringia*; both sexes at *Stachytarpheta* along borders of coffee plantations. Male aggressive, and sometimes territorial at flowers not claimed by larger, dominant species like *Lampornis hemileucus*. Frequently sallies for flies and gnats from perches in canopy or along edges and in gaps; gleans arthropods from foliage along edges and streams.

Breeding. Wet to early dry seasons, Aug or Oct-Mar in Costa Rica. During breeding season male perches in tall shrubs or subcanopy along edges of forest gaps, solitary or more often in leks up to 5. Nest is a small cup chiefly of treefern scales and spiderweb, decorated sparingly with bits of moss and lichen, 2-4 m up in shrub in understory or at forest edge, usually where protected from above by large overhanging leaves. Clutch size 2; incubation 16 days.

Movements. Most of population in Costa Rica moves to lower elevations following breeding, locally down to 400-600 m.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Costa Rica and Panama Highlands EBA. Fairly common over most of range, which includes several large protected areas, e.g. Tapanti National Park (Costa Rica).

Bibliography. Anon. (1998a), Blake (1958), Hernández-Baños *et al.* (1995), Renjifo *et al.* (1997), Ridgely & Gwynne (1989), Skutch (1967), Slud (1964), Stattersfield *et al.* (1998), Stiles (1985b, 1985c), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968a).

Genus *GOETHALSIA* Nelson, 1912

108. Pirre Hummingbird

Goethalsia bella

French: Colibri du Pirré **German:** Rotgesichtkolibri **Spanish:** Colibri del Pirre
Other common names: Rufous-cheeked/Goethals's Hummingbird

Taxonomy. *Goethalsia bella* Nelson, 1912. Cana, 2000 feet [c. 600 m], Panama. Considered a close relative of *Goldmania* and perhaps of *Hylocharis*, sharing with former the long, stiffened central undertail-coverts; behaviour and external morphology show similarities with *Eupherusa*. Monotypic.
Distribution. E Panama (Cerro Sapo and Cerro Pirre, in Darién) and extreme NW Colombia (Alturas de Nique, Chocó).



Descriptive notes. 8.4-9.5 cm; male 4 g, female 3 g. Male has straight black bill, with reddish mandible; forehead and lores rufous chestnut, upperparts metallic green; chin rufous chestnut, rest of underparts shining green; secondaries with buff patch; tail rufous tipped black, central pair of feathers green. Female similar to male but throat rufous buff, rest of underparts whitish. Immature similar to adult female.

Habitat. Forest and forest borders of foothills and mountain ranges between 600 and 1500 m; at Cerro Pirre, mostly found above 1000 m. Forages from near ground to mid-strata in the forest interior.

Food and Feeding. Feeds on flowering shrubs or small trees such as Ericaceae and Rubiaceae.

Breeding. No data available.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Currently considered Near-threatened. Restricted-range species: present in Darién Highlands EBA. Generally uncommon throughout its small range, and usually seen individually; abundance increases with altitude. Habitat on Cerro Pirre not threatened at present. A little-known species.

Bibliography. Anon. (1998a), Hilty & Brown (1986), Meyer de Schauensee (1982), Olog (1968), Ridgely & Gwynne (1989), Robbins *et al.* (1985), Somarriba (1984), Stattersfield *et al.* (1998), Sotz *et al.* (1996), Wetmore (1968a).

Genus *GOLDMANIA* Nelson, 1911

109. Violet-capped Hummingbird

Goldmania violiceps

French: Colibri à calotte violette **German:** Violettkeppenkolibri **Spanish:** Colibri de Goldman
Other common names: Goldman's Hummingbird

Taxonomy. *Goldmania violiceps* Nelson, 1911. Cerro Azul, 3000 feet [c. 1000 m], north-west of Chepo, Panama. Linked with *Goethalsia*, with which shares the long, stiffened central undertail-coverts; one proposal, based on external morphology, suggests placing present species in *Hylocharis*; general behaviour, however, indicates close affinities with *Chlorostilbon*. Monotypic.

Distribution. C Panama (Cerro Azul, Cerro Bruja, Cerro Tacarcuna) to extreme NW Colombia.



Descriptive notes. 8.5-9.5 cm; male 4-4 g, female 3-5. Male has straight black bill, lower mandible basally flesh-coloured; crown iridescent violet-blue; back and underparts metallic green; undertail-coverts green, with central feathers white and stiffened; tail slightly forked, maroon, broadly bordered with bronze; white femoral tufts. Female green above, whitish below, with grey spots on throat and green discs on sides; tail similar to male's, but tipped white. Immature resembles adult female.

Habitat. Humid forest and forest edges between 600 and 1200 m, commonest around 900 m. Forages mainly low down in dense undergrowth.

Food and Feeding. Nectar of low flowering shrubs, including *Salvia*, *Pachystachis*, *Palicourea* and *Psammisia*.

Breeding. Nests have been found Dec to Mar; no further information available.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Darién Highlands EBA. Fairly common to locally common (Cerro Azul and Cerro Jefe). Many parts of the montane habitats of this species as yet largely unaltered by man.

Bibliography. Anon. (1998a), Hilty & Brown (1986), Meyer de Schauensee (1982), Olog (1968), Ridgely & Gwynne (1989), Stattersfield *et al.* (1998), Sotz *et al.* (1996), Wetmore (1968a).

Genus *CYNANTHUS* Swainson, 1827

110. Dusky Hummingbird

Cyananthus sordidus

French: Colibri sombre **German:** Grauer Breitschnabelkolibri **Spanish:** Colibri Prieto

Taxonomy. *Cyanomyia* (?) *sordida* Gould, 1859. Oaxaca, Mexico.

Possibly forms a superspecies with *C. latirostris*; a reported hybrid of these two apparently refers to variation within adult male of present species. Monotypic.

Distribution. S Mexico, from Michoacan to Oaxaca.



Descriptive notes. 9-10 cm; 4.3-4.7 g. Male has slightly decurved bill, red, tipped black; crown dull green, auriculars blackish, rest of upperparts dull golden green, postocular stripe white, underparts dusky grey; tail slightly forked, greyish-green. Female similar to male, bill with upper mandible black, lower red tipped black; underparts paler; outer rectrices with blackish subterminal bar, tipped white. Immature resembles adult female but tips of outer rectrices pale buff.

Habitat. Open and semi-open arid areas with scattered trees and scrub, sometimes along roadsides or in flowering gardens, at 900-

2200 m. Forages in mid to upper strata.

Food and Feeding. No specific food plants have been recorded; presumably feeds on nectar of flowering *Agave*, *Castilleja* and *Opuntia*. Insects are caught in the air by hawking.

Breeding. Nests have been recorded Mar-May, Aug, Nov-Dec. When nesting, may be capable of adapting to more humid periods within its semi-arid habitat. Nest small, cup-shaped, placed in forks or attached to hanging twigs, built of soft plant material, exterior decorated with pieces of dead leaves, small twigs and cotton, but very seldom lichens. Clutch size 2. No further information.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Balsas Region and Interior Oaxaca EBA. Common throughout most of range; no threats noted to date. Readily accepts man-made habitats such as flowering gardens. Occurs at Cañón de Lobos (Morelos), Laguna San Felipe (Puebla), Sierra de Atoyac (Guerrero) and Monte Albán and Teotitlán del Valle (Oaxaca).

Bibliography. Anon. (1998a), Binford (1985, 1985), Friedmann *et al.* (1950), Howell & Webb (1995a), Hutto (1985), Johnson (1997), Mayr & Short (1970), Ridgway (1911), Rowley (1984), Stattersfield *et al.* (1998), Sotz *et al.* (1996), Wagner (1946a).

111. Broad-billed Hummingbird

Cyananthus latirostris

French: Colibri ciré **German:** Blaukehl-Breitschnabelkolibri **Spanish:** Colibri Piquiancho
Other common names: Doubleday's Hummingbird (*doubledayi*); Lawrence's Hummingbird (*lawrencei*)

Taxonomy. *Cyananthus latirostris* Swainson, 1827, tableland of Mexico; error = Valley of Mexico near Mexico City.

Possibly forms a superspecies with *C. sordidus*; a reported hybrid of these two apparently refers to variation within adult male of that species. Hybrids with *Agyrtia violiceps* and *Eugenes fulgens* documented suggest possible close relationship between these genera and *Cyananthus*. Race *doubledayi* sometimes considered a separate species; proposed race *tonoi* represents specimens from zone of intergradation between *propinquus* and *doubledayi*; proposed race *nitidus* is synonym of *doubledayi*. Race *lawrencei* has also been considered a distinct species. Racial differences mainly in male head coloration, though this may vary clinally, so number of valid races uncertain. Five subspecies recognized.

Subspecies and Distribution.

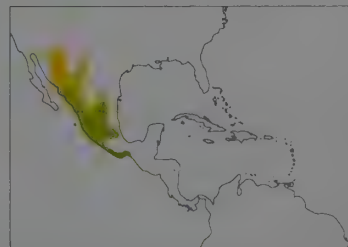
C. l. magicus (Mulsant & J. Verreaux, 1872) - S Arizona and SW New Mexico (SW USA) S to Nayari (CW Mexico).

C. l. latirostris Swainson, 1827 - San Luis Potosí and Tamaulipas to N Veracruz (EC Mexico).

C. l. lawrencei (Berlepsch, 1887) - Is Tres Marias (off W coast of Mexico).

C. l. propinquus R. T. Moore, 1939 - Guanajuato to Michoacan (C Mexico).

C. l. doubledayi (Bourcier, 1847) - Guerrero, Oaxaca and Chiapas (S Mexico).



Descriptive notes. 9-10 cm; 3.2-4.4 g. Male has straight bill, bright red with black tip; crown, nape and back emerald green; throat blue to violet-blue, rest of underparts metallic bronzy-green, undertail-coverts dusky white; tail slightly forked, blue-black with central rectrices tipped greyish. Female has white postocular stripe and dull green crown, back golden-green to emerald green; throat and underparts greyish; tail green to blue-green with subterminal blue-black band, tipped white. Immature resembles adult female; immature male has tail blue-black and underparts with blue and green patches. Race *magicus* has greenish

throat; *lawrencei* similar to nominate but throat turquoise-green in male, and tail is more deeply cleft; *propinquus* differs in darker coloration, crown metallic green, underparts bluish; *doubledayi* similar to nominate but forecrown of male iridescent blue-turquoise, throat deeper violet-blue, underparts generally bluer, undertail-coverts black.

Habitat. In USA, rocky canyons in deserts where natural streams or springs support vegetation; common vegetation used includes sycamore (*Platanus*) and mesquite (*Prosopis*). In Mexico, where found from sea-level to above 2000 m, habitat highly variable but typically arid to semi-arid bushy woodland, scrub and fairly open areas with some trees.

Food and Feeding. Forages on floral nectars of flowering *Agave*, *Caesalpinia*, *Castilleja* and *Opuntia*. Arthropod diet includes spiders, flies (Diptera), Hymenoptera and others.

Breeding. Breeding occurs in USA during peak flowering seasons between Apr and Sept; in Mexico breeding variable, possibly extending from Dec to Aug. In Arizona, nest density in a given area dependent upon nectar availability. Nest is cup-shaped, lined with soft downy plant material, exterior covered with leaves and bark (rarely lichens) glued in place with spiders' webs, 1.5-4 m above ground. Clutch size 2.

Movements. Migratory in USA and extreme N Mexico; resident elsewhere in its breeding range. N migrants winter S to N Guerrero; questionable reports of wintering in Oaxaca. Birds in USA begin arriving at some locations mid-Mar and depart by mid-Oct. Several extralimital records during breeding season likely to be result of post-breeding wandering; vagrant to Baja California, Oct-Jan.

Status and Conservation. Not globally threatened. CITES II. Common in USA; locally common to fairly common in Mexico. Despite use of a variety of habitats, their possible destruction may be a potential threat for the future throughout the species' range.

Bibliography. Arizmendi & Ornelas (1990), Baicich & Harrison (1997), Baltosser (1986a, 1989b), Bent (1940), Binford (1985, 1989), Blake & Hanson (1942), Brandt (1951), Contreras-Balderas (1997), Cottam & Knappen (1939), DeGraaf & Rappole (1995), Des Granges & Grant (1980), Friedmann *et al.* (1950), Gray (1958), Griscom (1934), Hejl *et al.* (1995), Howeli & Webb (1992b, 1995a), Johnsgard (1997), Kaufman (1996), Mayr & Short (1970), McCaskie (1970), Montgomerie (1979), Moore (1939a), Oberholser (1974), Parra *et al.* (1993), Phillips (1964), Phillips *et al.* (1964), Price *et al.* (1995), Ridgway (1911), van Rossem (1945a), Rowley (1984), Schaldach (1963), Short & Phillips (1966), Small (1994), Stotz *et al.* (1996), Wagner (1952, 1957b), Woodier (1998).

Genus *CYANOPHAI* Reichenbach, 1854

112. Blue-headed Hummingbird

Cyanophaia bicolor

French: Colibri à tête bleue

German: Blaukopfkolibri

Spanish: Colibrí Bicolor

Other common names: Wagler's Woodnymph

Taxonomy. *Trochilus bicolor* J. F. Gmelin, 1788, Guadeloupe; error = Dominica.

Relationships of genus unclear; nest type indicates affinities with *Chlorostilbon* and *Cyananthus*, voice with *Thalurania*. Monotypic.

Distribution. Dominica and Martinique.

Descriptive notes. 9-11 cm; male 4-7 g, female 4-5 g. Male has straight black bill, pinkish red on basal portion of lower mandible; head metallic violet-blue, back shining green, uppertail-coverts



deep blue; chin and throat violet-blue, rest of underparts metallic green, with faint blue gloss; tail forked, steel blue. Female has bill similar to male's, but entirely black; head shining green above, loreal and auricular region dusky, postocular spot dull grey; back bronze-green; underparts pale brownish-grey, bronze-green on sides; tail shining bronze at base, outer rectrices with broad steel blue sub-terminal band and large grey tips. Immature like adult female but head feathers pale green with brown fringes.

Habitat. Virgin forest, forest edges and along secondary growth of rivers in the mountains.

Rare at sea-level. Most numerous between 800 and 1000 m.

Food and Feeding. Nectar of flowering plants from ground to tree tops, such as *Pachystachys*, *Asclepias*, *Begonia*, *Costus*, *Besleria*, *Duranta* and *Inga*. Sallies for insects over mountain streams or collects arthropods from leaves.

Breeding. Mar-May. Cup-shaped nest of fine plant fibres like fluff from silk-cotton tree or brown soft parts from outer cover of tree ferns, placed at height of 1-4 m on horizontal twigs or fern fronds. Usually decorated with attached strips of dead leaves from *Heliconias* and ferns. Clutch size 2; incubation 16-18 days, by female; chick flesh-coloured with pale grey dorsal down; fledging period 20-23 days; young remain with female for 3-4 weeks. First breeding in second year.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Lesser Antilles EBA. Patchy distribution on both islands. Densities in rainforest between Fort-de-France and Morne Rouge, Martinique, at least 3-4 individuals/km². Formerly more numerous on Dominica but hurricanes in the early 1980's almost extirpated the local population, which is now slowly recovering.

Bibliography. Anon. (1998a), Bon Saint Côme (1982), Bond (1985), Ingels (1976a), Raffaele *et al.* (1998), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Tyrrell & Tyrrell (1990).

PLATE 55

inches 2
cm 5



Genus *THALURANIA* Gould, 1848

113. Mexican Woodnymph

Thalurania ridgwayi

French: Dryade du Mexique German: Mexikonympe Spanish: Zafiro Mexicano

Taxonomy. *Thalurania ridgwayi* Nelson, 1900, San Sebastian, Jalisco, Mexico. Forms a superspecies with *T. colombica*, *T. fannyi* and *T. furcata*; species limits unclear, and all four have been considered conspecific. Alternatively, blue-crowned present species often considered a race of purple-crowned *T. colombica*. Monotypic.

Distribution. Pacific slope of Mexico, in S Nayarit, Jalisco and Colima.



Descriptive notes. 9-10 cm; male 3.5-4.2 g, female c. 3.5 g. Male has straight black bill; forehead iridescent violet-blue, hindcrown bluish-green, rest of upperparts green; throat iridescent emerald green, belly and undertail-coverts dusky green; tail slightly forked, bluish-black. Female upperparts similar to male, small white postocular spot; below greyish, side of breast with some green discs; tail slightly forked, bluish-black, central pair of rectrices with greenish shine, outer rectrices tipped white. Immature unknown.

Habitat. Humid forest, canyons and foothills at 250-1200 m; exact habitat requirements are

still unknown; probably also occurs in coffee plantations.

Food and Feeding. No specific food plants have been recorded, but presumably feeds on nectar of flowering Rubiaceae, Zingiberaceae and epiphytes (bromeliads, Ericaceae and mistletoes) like other *Thalurania*. Arthropods are gleaned from foliage and caught in the air by hawking.

Breeding. Birds in breeding condition collected Feb-Mar. No further information.

Movements. Sedentary.

Status and Conservation. VULNERABLE. CITES II. Restricted-range species: present in North-west Mexican Slope EBA. Rare to locally common. Frequently recorded at Puerto Los Mazos, on lower slope of Sierra de Manantlán Biosphere Reserve (Jalisco/Colima); also occurs in other protected areas e.g. Cerro San Juan Biosphere Reserve (Nayarit) and Nevados de Colima National Park (Jalisco/Colima). Although exact habitat requirements have not been documented, species is probably bound to forest habitats, which are under severe threat of destruction, though some suitable areas remain intact. Without more precise knowledge of ecological requirements, conservation planning is barely feasible; further investigation into life history urgently required.

Bibliography. Anon. (1998a), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Escalante & Peterson (1992), Friedmann *et al.* (1950), Hernández-Baños *et al.* (1995), Howell & Webb (1995a), Johnson (1997), Phillips (1961), Ridgway (1911), Schladach (1963), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Wege & Long (1995).

114. Purple-crowned Woodnymph

Thalurania colombica

French: Dryade couronnée German: Violetttronennympe Spanish: Zafiro Coroniazul
Other common names: Violet-crowned/Crowned Woodnymph: Colombian Woodnymph (*colombica*); Blue-crowned Woodnymph (*townsendi*)

Taxonomy. *Ornismya colombica* Bourcier, 1843, San Agustín, Magdalena Valley, Colombia. Forms a superspecies with *T. ridgwayi*, *T. fannyi* and *T. furcata*; species limits unclear, and all four have been considered conspecific. Alternatively, purple-crowned present species often treated as conspecific with blue-crowned *T. ridgwayi*, and sometimes also with green-crowned *T. fannyi*, forming a group with glittering crowns and more violet on back, as opposed to mostly dull-crowned, green-backed forms of *T. furcata*. Lump of present species with *T. fannyi* supported by their close similarity, and also by blue feathering at rear of crown in *T. fannyi*, a feature decreasing with distance from adjacent purple-crowned forms of present species; females too are very similar. Race *hypochlora* of *T. fannyi* may belong in present species. Race *rostrifera* may be inseparable from nominate. Race *townsendi* (with *venusta*) might be approaching separate species status. Four subspecies recognized.

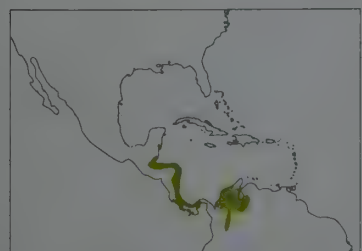
Subspecies and Distribution.

T. c. townsendi Ridgway, 1888 - E Guatemala to SE Honduras.

T. c. venusta (Gould, 1851) - E Nicaragua to C Panama.

T. c. colombica (Bourcier, 1843) - N Colombia (S to head of Magdalena Valley) and NW Venezuela.

T. c. rostrifera Phelps & Phelps, Jr., 1956 - NW Venezuela (SW Táchira).



Descriptive notes. Male 9.5-10.5 cm, 4.3-4.6 g; female 8.5-9 cm, 3.9-4.1 g. Bill black, feet dark grey. Male has forehead and crown, belly and upper back violet, throat and chest glittering green, nape dark bronzy-green, lower back and rump dark bluish-green, tail blue-black and deeply forked. Female is bright green above, pale grey on the throat and chest and darker grey on the belly; the distal half of the tail is blue-black with the outer 3 rectrices white-tipped. Immature male of all races dull dusky green to bronze-green on crown and underparts, no glittering green or violet, tail shorter and less forked than those of adults; immature female

duller and bronzier green above with narrow buff fringes on face, nape and rump feathers. Race *rostrifera* differs mainly in longer bill; in *venusta*, male is larger and longer-tailed with the nape very dark blue-green, female has belly much darker, dusky grey glossed with green; in *townsendi* male has violet below restricted to sides, with green belly and bronzy nape, female dark grey below.

Habitat. Humid forest and adjacent edges, tall second growth and semi-open (cacao plantations, shaded gardens) vegetation, avoids open, scrubby areas. During breeding season male mainly in canopy, female more in understorey; at other times both sexes occur at all heights, lower along edges. Breeds from sea-level to 750-900 m (Costa Rica), 1600-1900 m (Colombia and Venezuela).

Food and Feeding. Visits flowers of a wide variety of epiphytes (bromeliads, Ericaceae, mistletoes, gesneriads, Marcgraviaceae), shrubs and small trees (*Besleria*, *Hamelia*, *Cephaelis*, *Cornutia*, *Acanthaceae*), less often those of larger trees like *Inga*; also fond of flowers of large herbs like *Heliconia* and *Costus*; prefers to visit flowers under partial to closed canopy rather than in open, male notably aggressive and frequently territorial at rich clumps of flowers. Frequently flycatches by sallying from perch in canopy or along edge or gap, also (especially female) gleans arthropods from foliage.

Breeding. Mainly during dry season (Feb-Jun) in Costa Rica; Mar-Jul or Aug, perhaps later, in N and C Colombia. Male may defend rich flowers to attract female. Nest a compact cup of treefern scales, plant down and cobweb, decorated on outside with lichens and moss, on horizontal twig of shrub under overhanging leaf, in forest; often at edge of small gap or trail, 1-5 m above ground.

Movements. In Costa Rica, part of population moves upslope to 1000-1200 m following breeding; also local movements following shifts in flowering. No information for other areas.

Status and Conservation. Not globally threatened. CITES II. One of the commonest forest hummingbirds over most of range, but suffering considerable habitat loss due to deforestation in many areas, notably parts of Central America and N Colombia. Occurs in several protected areas, e.g. Carara Biological Reserve, Gofito National Wildlife Refuge, and Corcovado and Braulio Carrillo National Parks (Costa Rica).

Bibliography. Ayala (1986), Chapman (1917, 1926), Escalante & Peterson (1992), Fogden (1993), Griscom (1932a), Hilty & Brown (1986), Howell, S.N.G. & Webb (1995a), Howell, T.R. (1957), Johnson (1997), Land (1970), Matheus *et al.* (1996), Meyer de Schauensee & Phelps (1978), Monroe (1968), Phelps & Phelps (1956), Ridgely & Gwynne (1989), Ridgway (1911), Skutch (1981), Slud (1960, 1964), Stiles (1975, 1980, 1985b, 1995a, 1995b), Stiles & Skutch (1989), Stone, J.L. (1996), Stone, W. (1932), Stotz *et al.* (1996), Todd & Carriker (1922), Weathers & Stiles (1989), Wetmore (1968a).

115. Green-crowned Woodnymph

Thalurania fannyi

French: Dryade de Fanny German: Grüntronennympe Spanish: Zafiro Coroniverde
Other common names: Emerald-bellied Woodnymph (*hypochlora*)

Taxonomy. *Trochilus Fannyi* DeLattre and Bourcier, 1846, Río Dagua, near Buenaventura, Colombia. Forms a superspecies with *T. ridgwayi*, *T. colombica* and *T. furcata*; species limits unclear, and all four have been considered conspecific. Alternatively, green-crowned present species sometimes considered conspecific with blue-crowned *T. ridgwayi* and purple-crowned *T. colombica*; this lump supported by great similarity of these forms, apart from crown colour of male, and indeed male of present species shows some blue feathering at rear of glittering green crown which decreases with distance from adjacent purple-crowned forms; also female plumages of present species and *T. colombica* very similar. Distinctive race *hypochlora* may be a separate species, or possibly referable to *T. colombica*. Race *subtropicalis* may not be distinguishable from *verticeps*. Four subspecies tentatively recognized.

Subspecies and Distribution.

T. f. fannyi (DeLattre & Bourcier, 1846) - E Panama and extreme NW to SW Colombia.

T. f. subtropicalis Griscom, 1932 - WC Colombia, in Cauca Valley and along adjacent W & C Andes.

T. f. verticeps (Gould, 1851) - Pacific slope of W Andes of extreme SW Colombia and NW Ecuador.

T. f. hypochlora Gould, 1871 - Pacific lowlands of Ecuador.



Descriptive notes. Male 9.5-10.5 cm, 4-7 g; female 8.5-9 cm, 4-2 g. Bill black, feet dusky grey in both sexes. Male has throat, chest and crown glittering green, the crown more bluish-green towards rear, sometimes with a few glittering blue-violet feathers along the hind margin; nape is dark bronze to bronze-green, most of the back and uppertail-coverts dark green to bronze-green; belly and a band across the upper back, violet; undertail-coverts more or less fringed with whitish, tail blue-black and deeply forked. Female green above, often more bronze-green on the crown and nape, with the shoulders usually distinctly blue; throat and upper breast very pale grey, belly dark dusky grey glossed with dark green; vent and undertail-coverts more or less whitish, tail blue-black with the outer 3 rectrices tipped with white. Immature male dull dusky bronze-green on crown and underparts with no glittering green or violet, tail shorter and less forked; immature female duller and bronzier green above with narrow buff fringes to feathers on face, nape and rump. In race *subtropicalis*, male similar but with nape more bronzy, less violet on back, and tail shorter and less forked, while female has paler grey belly; these tendencies further accentuated in *verticeps*; in race *hypochlora* male has belly mostly green with little violet, female uniform pale grey below.

Habitat. Humid forest and adjacent edges, tall second growth and semi-open habitats (cacao plantations, shaded gardens), avoids open, scrubby areas; in forest occurs from understorey to lower part of canopy. Breeds from sea-level locally to 1200 m on the Pacific slope, and at 800-1900 m on the slopes of the Cauca Valley in Colombia.

Food and Feeding. As far as known, visits a similar range of flowers as *T. colombica*, including those of epiphytes (especially bromeliads, Ericaceae and mistletoes), shrubs and mostly small trees (*Besleria*, *Hamelia*, *Cephaelis*, *Palicourea*, *Aphelandra*, *Inga*), large herbs like *Heliconia* and *Costus*; prefers flowers under partial to closed canopy rather than in open; males notably aggressive and frequently territorial at rich clumps of flowers. Frequently flycatches by sallying from perch in canopy or along edge or gap, also (especially female) gleans arthropods off foliage.

Breeding. Feb-Sept in NW Colombia, Jan-Nov in SW Colombia. Nest a downy cup saddled on slender fork or twig 1-3 m (occasionally to 8 m) up in tall grass or shrubbery at forest edge or inside forest. Male may defend rich clumps of flowers to attract females. Clutch size 2. No further information.

Movements. No information available.

Status and Conservation. Not globally threatened. CITES II. Common to abundant in forested parts of Pacific slope of Colombia; more local and less numerous on slopes overlooking Cauca Valley, but able to use disturbed or fragmented forest in many areas. Severe deforestation of W Ecuadorian lowlands may well threaten the distinctive race *hypochlora*, on which more information is urgently required.

Bibliography. Becker & López (1997), Bertin & Wilzbach (1979), Best *et al.* (1997), Chapman (1926), Cook (1996), Escalante & Peterson (1992), Hilty (1997), Hilty & Brown (1986), Kirwan & Marlow (1996), Meyer de Schauensee (1949), Parker *et al.* (1995), Pople *et al.* (1997), Ridgely & Gwynne (1989), Robbins & Ridgely (1990), Salaman & Mazariegos (1998b), Stotz *et al.* (1996), Wetmore (1968a), Williams & Tobias (1994).

116. Fork-tailed Woodnymph

Thalurania furcata

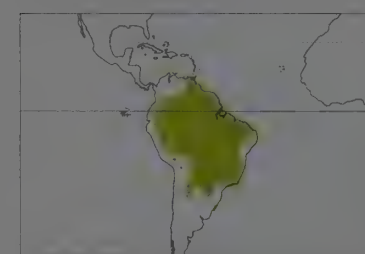
French: Dryade à queue fourchée **German:** Schwalbennympe **Spanish:** Zafiro Golondrina
Other common names: Princess/Common/Cayenne Woodnymph

Taxonomy. *Trochilus furcatus* J. F. Gmelin, 1788, Cayenne.

Forms a superspecies with *T. ridgwayi*, *T. colombica* and *T. fannyi*; species limits unclear, and all four have been considered conspecific. Alternatively, mostly dull-crowned and more green-backed forms are sometimes separated in present species from the other three lumped as another species with glittering crowns and more violet on back. Of the races currently recognized, most are based on variations in coloration of adult male, and several doubtfully valid. Races *baeri* and *eriphile*, with glittering green frontlets, were in past separated as *T. eriphile*, but former intergrades with adjacent dull-crowned races in Brazil, indicating potential pitfalls of attributing taxonomic significance to this feature. Race *jelskii* represents zone of intergradation of *viridipectus*, *simoni* and *boliviana*; *furcatoides* intergrades with *balzani* and *baeri* where their ranges meet in NC & C Brazil. "*Thalurania lerchi*", known from Bogotá trade skins, is apparently a hybrid between present species and *Chrysoronia oenone*; "*Eucephala scapularia*", known from single specimen from French Guiana, is probably a hybrid of present species with *Chlorostilbon notatus*. Name *tschudii* should perhaps replace *jelskii*; if so, *jelskii* may be correct name for current race *boliviana*. Proposed race *taczanowskii* (NE Peru) not reliably separable from *viridipectus*. Thirteen subspecies recognized.

Subspecies and Distribution.

T. f. refulgens Gould, 1853 - NE Venezuela; erroneously reported from Trinidad.
T. f. furcata (J. F. Gmelin, 1788) - extreme E Venezuela, the Guianas and NE Brazil (N of Amazon).
T. f. fissilis Berlepsch & Hartert, 1902 - E Venezuela and adjacent extreme W Guyana and NE Brazil.
T. f. orenocensis Hellmayr, 1921 - upper Orinoco region of S Venezuela.
T. f. nigrofasciata (Gould, 1846) - SE Colombia, NW Brazil (upper R Negro) and extreme S Venezuela.
T. f. viridipectus Gould, 1848 - E foothills of Andes and adjacent lowlands of E Colombia, E Ecuador and NE Peru.
T. f. jelskii Taczanowski, 1860 - most of E Peru and adjacent Brazil.
T. f. simoni Hellmayr, 1906 - upper Amazon region (S of Amazon) in extreme E Peru and W Brazil.
T. f. balzani Simon, 1896 - NC Brazil (S of Amazon).
T. f. furcatoides Gould, 1861 - lower Amazon region of E Brazil (S of Amazon).
T. f. boliviana Boucard, 1894 - Andean foothills and adjacent lowlands of SE Peru and NE Bolivia.
T. f. baeri Hellmayr, 1907 - NE & C Brazil to SE Bolivia and NW & NC Argentina.
T. f. eriphile (Lesson, 1832) - SE Brazil, adjacent Paraguay and NE Argentina (Misiones).



Descriptive notes. Male 9.5-10.5 cm, 4-8 g; female 8-9 cm, 4-2 g. Straight medium-sized bill black. Male mostly dark bronzy-green above with crown and nape dark dusky-bronze; throat is glittering green, the belly and a band across the upper back violet; tail blue-black and forked, undertail-coverts dark steely blue edged broadly with dull white. Female bright green above, duller and more bronze on the crown, and pale grey below; the distal part of the tail is steely blue-black, the outer 3 rectrices white-tipped. Immature male nearly uniform dusky bronze-green below and dull bronze-green above; immature female averages more bronzy-green

above than adults and usually shows some pale buffy fringes on face, nape and rump feathers. Race *fissilis* differs mainly in longer bill and (male) solid blue undertail-coverts; in *nigrofasciata* and *verticeps* band of violet across upper back interrupted medially, and green of throat more extensive and separated from violet belly by a band of black, usually broader in the former; *nigrofasciata* is more golden green, *verticeps* more bluish-green above; *viridipectus* has green of gorget extending onto breast, bordered narrowly below with black; *jelskii* has lower throat and breast more or less tinged with blue and black band usually interrupted, basically representing an intergradation towards *boliviana*, in which green is restricted to gorget and black reduced to lateral patches or lacking; *furcatoides* differs from nominate mainly in larger size and more blackish crown; *balzani* has crown green, undertail-coverts usually pure white; *simoni* represents a zone of intergradation between *balzani* and *jelskii*-*boliviana*, being most like former but with dark central stripe on vent and undertail-coverts; *baeri* and *eriphile* have glittering green frontlets contrasting with blackish crowns, the former intergrading with the adjacent *furcatoides* and *balzani* where their ranges meet. Racial variation in females involves darkness of grey underparts, with some variation in lateral green scaling, colour and pattern of undertail-coverts, colour of crown and shade of green above, in general paralleling variations in their respective males.

Habitat. Humid forest (both *terra firme* forest and *várzea* in Amazonia) and forest edge, taller second growth and semi-open, shaded plantations and gardens; possibly in more scrubby habitats in some parts of range but more detailed information lacking.

Food and Feeding. Visits flowers of epiphytes (bromeliads, ericads), vines (*Mucuna*, *Gurania*), lianas (*Combretum*), trees (*Inga*, *Erythrina*, *Genipa*, *Tachigali*, *Quararibea*, *Syzgium*), shrubs (especially Rubiaceae, Acanthaceae) and large herbs (*Heliconia*, *Costus*) in forest and edge habitats in E Colombia; also obtains arthropods by flycatching and, less often, foliage-gleaning. Small flies and wasps important in diet with smaller numbers of ants, other insects and spiders.

Breeding. Birds in breeding condition recorded Apr-Oct in foothills of E Andes, Aug-Oct along the Amazon in E Colombia (*viridipectus*). No further information.

Movements. No information available; presumably more or less sedentary except for local movements following shifts in flowering; populations in Andean foothills may move altitudinally.

Status and Conservation. Not globally threatened. CITES II. Common over most of its wide range but populations in some areas are or may soon be threatened by deforestation, especially parts of Brazil, Colombia and Paraguay. In Brazil, occurs in several protected areas, e.g. Serra dos Órgãos and Brasília National Parks.

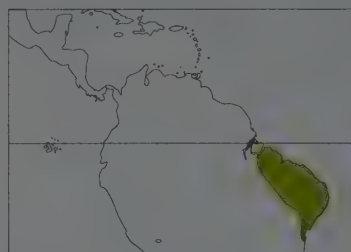
Bibliography. Blake (1950b), Bond & Meyer de Schauensee (1943), Butler (1979), Canevari *et al.* (1991), Chubb (1910), Cintra & Yamashita (1990), Contreras & Contreras (1990), Contreras *et al.* (1990), Cory (1918), Cotton (1993, 1998a), Friedmann (1948), Gilliard (1941), Grantsau (1988), Gyldestolpe (1945b), Hartert (1922), Haverschmidt & Mees (1994), Hayes (1995), Hellmayr (1908, 1929), Hilty & Brown (1986), Marini *et al.* (1997), Meyer de Schauensee & Phelps (1978), Olrog (1963c), Oniki (1996), de la Peña (1994), Perry *et al.* (1997), Phelps & Phelps (1958), Pinto (1947), Reimser & Traylor (1989), Ruschi (1981-1982, 1986), Rutgers & Norris (1972), Saibene *et al.* (1996), Short (1975), Sick (1993, 1997), Sneathale (1907, 1909, 1913), Snyder (1966), Stotz *et al.* (1996), Stouffer & Bierregaard (1995), Tostain *et al.* (1992), Willard *et al.* (1991), Willis (1992), Zimmer (1950c).

117. Long-tailed Woodnymph

Thalurania watertonii

French: Dryade de Waterton **German:** Langschwanznympe **Spanish:** Zafiro Colilargo
Other common names: Waterton's Woodnymph

Taxonomy. *Trochilus Watertonii* Bourcier, 1847, Miribi Creek, near Essequibo River, Guyana. Forms a superspecies with *T. glaucopsis*; probably old elements within genus *Thalurania*. Monotypic.
Distribution. E Brazil (E Pará to Pernambuco and Bahia); possibly also Guyana, where known only from type specimen.



Descriptive notes. Male c. 13 cm (including tail of 6 cm), female c. 10 cm; 4-6.5 g. Male has medium-sized straight bill, black; crown and lower neck green, back iridescent violet-blue; underparts shining grass green, flanks violet-blue; tail long, deeply forked, steel blue. Female has crown and hind neck golden green, lower back bluish-green; uniformly greyish-white below; tail not elongated, slightly forked, central pair of rectrices blue-green, rest green with broad, steel blue subterminal band and white tips. Immature similar to adult female, duller grey below, head feathers with buffy fringes.

Habitat. Coastal rainforest, *cerrado*, semi-open clearings, plantations and parks, from sea-level to 500 m. Forages at low to medium heights, usually at the periphery of vegetation.

Food and Feeding. Nectar of flowering vines, cacti, epiphytes, shrubs and trees, such as Passifloraceae, Cactaceae, Bromeliaceae, Loranthaceae, Verbenaceae, Rubiaceae, Leguminosaceae. Sometimes individuals cling to long corollas while feeding. Insects are caught in the air by hawking. Male establishes feeding territories which are aggressively defended against intraspecific and interspecific intruders.

Breeding. Nov-Feb. Cup-shaped nest of fine rootlets and moss, held together by cobweb, is built on horizontal branch in shrub or small tree, usually protected by overhanging leaves, 1.5-2.5 m above ground. Clutch size 2; incubation 14-15 days, by female; chick darkish with two rows of buffy greyish dorsal down; fledging at c. 20 days. First breeding in second year.

Movements. Sedentary, some inland wandering during flowering season.

Status and Conservation. Not globally threatened. CITES II. Common throughout range; seems to accept man-made habitats where patches of forest or stands of scattered trees remain. Common on Brazilian side of Iguaçu Falls, with density of at least 2-3 pairs/km². Occurs in Monte Pascoal National Park, Bahia, and Pedra Talhada State Park, Alagoas.

Bibliography. Butler (1926a), Forrester (1993), Grantsau (1988), Meyer de Schauensee (1982), Pacheco & Whitney (1995), Pinto (1935), Ruschi (1981-1982, 1982a, 1986), Rutgers & Norris (1972), Sargeant (1996), Sick (1993, 1997), Snyder (1966), Stotz *et al.* (1996), Willis (1992).

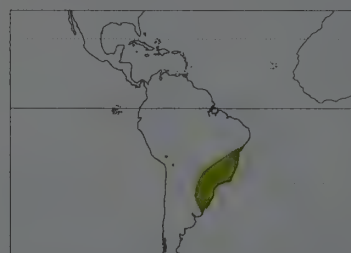
118. Violet-capped Woodnymph

Thalurania glaucopsis

French: Dryade glaucope **German:** Blaukronennympe **Spanish:** Zafiro Capirotado
Other common names: Blue-crowned/Blue-headed/Brazilian Woodnymph

Taxonomy. *Trochilus glaucopsis* J. F. Gmelin, 1788, Brazil.

Forms a superspecies with *T. watertonii*; probably old elements within genus *Thalurania*. Monotypic.
Distribution. E & S Brazil (Bahia to Rio Grande do Sul), E Paraguay and NE Argentina; doubtfully N Uruguay.



Descriptive notes. 8-11 cm; male 5-0 g, female 4-0 g. Male has bill straight, medium-sized, almost blackish or with dark brown tip to lower mandible; cap glittering violet-blue; upperparts dark golden green; underparts brilliant green; undertail-coverts greenish to bluish, laterally greyish-brown; tail forked, steel blue. Female lacks contrasting cap; underparts including undertail-coverts dirty white to pale buff; tail only slightly forked; inner rectrices metallic green, outer rectrices steel blue with whitish tips. Immature male has turquoise-blue cap, with or without scattered violet-blue feathers; throat feathers with whitish subterminal

bars; greyish-brown areas on breast, belly and undertail-coverts.

Habitat. Virgin forest, forest edges, scrub; also found in suburban areas like parks and gardens, and even within city centres. Ranges from near sea-level to 850 m.

Food and Feeding. Forages for nectar at a great variety of native and introduced plants. In forested areas, plant families include epiphytes like Bromeliaceae (*Vriesea*), Orchidaceae, Marantaceae, Musaceae, Passifloraceae, Leguminosae (*Dahlstedtia*), Zingiberaceae, Rubiaceae, Bombacaceae, Vochysiaceae, Strelitziaceae, *Heliconia*; in gardens, Malvaceae (*Hibiscus*, *Abutilon*), Euphorbiaceae (*Poinsettia*), Crassulaceae (*Kalanchoe*), Fabaceae (*Erythrina*); various tree species, including *Citrus*, *Anacardium*, *Dombeya* and *Eucalyptus*. Feeds also on small insects that are caught by gleaning or hawking.

Breeding. Oct-Feb. Nest bowl-shaped, made of soft plant wool and fibres, such as Gramineae, *Typha*, Bombacaceae, or Bromeliaceae; external "decoration" includes fern scales and lichen; placed on a horizontal branch or in twig fork in tree such as *Chusquea*, 1.5-3 m above ground. Clutch size 2; incubation 15 days, by female; fledging period 20-25 days.

Movements. Short-distance migrant. Although sometimes listed for Uruguay, no recent confirmation of breeding, leaving southern limits of distribution unclear; perhaps only occurs as migrant.

Status and Conservation. Not globally threatened. CITES II. One of commonest trochilids in SE Brazil, where frequent both in forested and semi-open areas; occurs in several protected areas, e.g. Serra dos Órgãos and Itatiaia National Parks. In Paraguay, known only from Alto Paraná region; in Argentina, found in humid lowlands of Misiones.

Bibliography. Belton (1984), Berlioz (1930a, 1931a, 1934, 1964, 1965), Brooks *et al.* (1993), Canevari *et al.* (1991), Forrester (1993), Grantsau (1988), Guix *et al.* (1992), Hayes (1995), Laubmann (1940), Lowen, Bartrina, Clay & Tobias (1996), Lowen, Clay *et al.* (1995), Marini *et al.* (1997), Naroosky & Yzurietta (1993), Navas & Bo (1993), Oniki (1996), Parker & Goerck (1997), de la Peña (1994), do Rosário (1996), Ruschi (1949b, 1973d, 1976d, 1981-1982, 1986), Rutgers & Norris (1972), Saibene *et al.* (1996), Sargeant (1996), Scott & Brooke (1985), Sick (1993, 1997), Sick & Teixeira (1981), Snow & Snow (1986), Sosa (1937), Stotz *et al.* (1996), Tobias *et al.* (1993), Willis (1992).

Genus *DAMOPHILA* Reichenbach, 1854

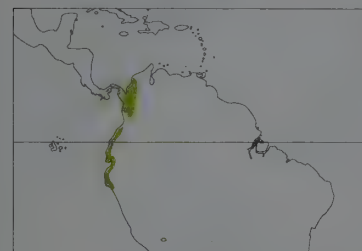
119. Violet-bellied Hummingbird

Damophila julie

French: Colibri julie **German:** Juliakolibri **Spanish:** Colibrí de Julia
Other common names: Julie's Hummingbird

Taxonomy. *Ornismya* [sic] *julie* Bourcier, 1842, Tunja, Colombia. Affinities unclear; genus possibly close to *Thalurania* or *Chlorostilbon*. Three subspecies recognized. **Subspecies and Distribution.**

D. j. panamensis Berlepsch, 1884 - C Panama (Canal Zone, both slopes of Darién); also reported, apparently in error, from Costa Rica.
D. j. julie (Bourcier, 1842) - N & C Colombia. E to Santa Marta, Magdalena Valley and Tolima.
D. j. feliciana (Lesson, 1844) - SW Colombia (Nariño) through W Ecuador to NW Peru (Tumbes).



Descriptive notes. 8.1-9.2 cm; male 3.3-3.5 g, female 2.5-3 g. Male has short straight bill, upper mandible black, lower pinkish, tipped black; iridescent green crown, back shining green; gorget glittering green, belly iridescent violet-blue; tail rounded, bluish-black. Female above similar to male, below greyish-white, outermost pair of rectrices tipped grey. Immature male like adult female, often with some blue spots on belly. Race *panamensis* has crown green like back; *feliciana* has longer bill, crown brilliant green, belly violet.

Habitat. Lowland forest, forest edge, second growth, clearings, common in semi-open forest, occasionally in canopy when trees are in flower. Sometimes participates in mixed species flocks.

Food and Feeding. Nectar of flowering shrubs and trees, including Rubiaceae, Ericaceae, Gesneriaceae (*Besleria*) and *Inga*. Insects are caught in the air by hawking. Male establishes territories at nectar-rich food sources.

Breeding. Jan-Jul (Panama), Nov-May (Colombia, Ecuador). Cup-shaped nest of plant down is saddled on small branches of bushes at 1.5-4.2 m above the ground. Clutch size 2; incubation c. 15 days, by female; chick has two rows of grey-buff dorsal down; fledging period 20-22 days.

Movements. Sedentary, with some seasonal altitudinal dispersal, usually after reproduction. **Status and Conservation.** Not globally threatened. CITES II. Widespread and fairly common in coastal lowlands. Some local populations protected, e.g. in Tayrona and Los Katíos National Parks (Colombia) and Río Palenque Science Centre (Ecuador). Until mid-1970's, species was common in international bird trade, but this has now ceased.

Bibliography. Anon. (1998a), Berg (1994), Best *et al.* (1997), Brosset (1964), Butler, A.L. (1928), Butler, T.Y. (1979), Darlington (1931), Gloger (1987), Hallinan (1924), Hilty & Brown (1986), Parker, Parker & Plenge (1982), Parker, Schulenberg *et al.* (1995), Pople *et al.* (1997), Ridgely & Gwynne (1989), Rousseau-Decelle (1931), Slud (1964), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968a), Williams & Tobias (1994), Willis & Eisenmann (1979).

Genus *LEPIDOPYGA* Reichenbach, 1855

120. Sapphire-throated Hummingbird

Lepidopyga coeruleogularis

French: Colibri faux-saphir **German:** Blaukehlkolibri **Spanish:** Colibrí Gorgizafiro
Other common names: Duchassain's Hummingbird

Taxonomy. *Trochilus* (—?) *coeruleogularis* Gould, 1851, David, Chiriquí, Panama. Closely related to *Damophila*, and sometimes placed therein. *L. lilliae* sometimes considered a race, morph or age stage of present species. Race *confinis* occasionally considered synonymous with nominate. Three subspecies recognized.

Subspecies and Distribution.
L. c. coeruleogularis (Gould, 1851) - Pacific slope of W Panama from Chiriquí to Canal Zone.
L. c. confinis Griscom, 1932 - E Panama (Caribbean slope of Darién) and adjacent NW Colombia.
L. c. coelina (Bourcier, 1856) - N Colombia, from N Chocó through Ciénaga Grande to Santa Marta.



Descriptive notes. 8.5-9.5 cm; 3.9-4.3 g. Male has straight short bill, upper mandible black, lower pinkish, tipped black; upperparts shining green, coppery on rump; throat and chest iridescent violet-blue, rest of underparts glittering green; tail forked, central rectrices coppery gold, rest blue-black. Female similar to male but greyish-white below, bluish-green spots on sides, outer rectrices tipped white. Immature like adult female, buffy fringes on head feathers. Race *confinis* darker green on upper back, with chin and throat glittering turquoise; *coelina* less bronzy above, with blue throat.

Habitat. Shrubby vegetation, open groves, forest edge, mangroves, coastal lowland up to 100 m in Santa Marta, N Colombia. Usually forages rather low down inside semi-open shrub habitat; may also be seen in canopy when trees are in flower.

Food and Feeding. Nectar of flowering shrubs and trees like Leguminosaceae and Myrtaceae. Arthropods are gleaned from branches and leaves, and occasionally flying insects are caught by hawking. During peak of blooming season several individuals may be seen together in flowering trees.

Breeding. Jan-Mar (Panama, N Colombia), but nests have also been found in Jul (Colombia). Small deeply-cupped nest is built openly in forks of low shrubs, of dry light-coloured plant down, externally decorated with lichen and pieces of dead leaves, c. 0.7-1.5 m above the ground. Clutch size 2; incubation 15-16 days, by female; chick is flesh-coloured with two rows of cinnamon dorsal down; fledging period 19-22 days.

Movements. Sedentary; local altitudinal dispersal likely to occur. **Status and Conservation.** Not globally threatened. CITES II. Common resident in coastal Darién (Panama) and Santa Marta region (Colombia). Readily accepts man-made habitats. Part of range protected, e.g. in Los Katíos and Tayrona National Parks (Colombia). **Bibliography.** Anon. (1998a), Griscom (1932b), Hilty & Brown (1986), Meyer de Schauensee (1982), Olrog (1968), Olson (1997), Ridgely & Gwynne (1989), Rodríguez (1982), Slud (1964), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968a), Willis & Eisenmann (1979).

121. Sapphire-bellied Hummingbird

Lepidopyga lilliae

French: Colibri de Lilliane **German:** Blaubauchkolibri **Spanish:** Colibri Ventrifaziro

Taxonomy. *Lepidopyga lilliae* Stone, 1917, Punto Caimán, Santa Marta, Colombia. Status uncertain: sometimes considered a race, morph or age stage of *L. coeruleogularis*. Monotypic. **Distribution.** Coastal NC Colombia, around Ciénaga Grande and near mouth of R Ranchería, Riohacha (Guajira).



Descriptive notes. 8.9-9.4 cm; male 4-3 g. Male has short straight bill, upper mandible black, lower pinkish tipped black; upperparts blue-green, underparts rich blue with iridescent violet throat; tail deeply forked, blue-black. Female and immature unknown.

Habitat. Occupies coastal mangroves, though also occasionally seen in xerophytic shrub vegetation. Mainly seen alone at various heights within mangroves.

Food and Feeding. Not known; most likely nectar and insects as other hummingbirds. **Breeding.** No information.

Movements. Unknown, most likely sedentary.

Status and Conservation. CRITICALLY ENDANGERED. CITES II. Restricted-range species; present in Caribbean Colombia and Venezuela EBA. A rare species endemic to N Colombian mangrove swamps, a habitat destroyed on large scale since 1970's by coastal highway and pipeline construction, leading to disruption of tidal flow. Species occurs within two major protected areas: Isla de Salamanca National Park (21,000 ha) and Ciénaga Grande de Santa Marta Sanctuary (23,000 ha). Research and survey work required before adequate protective measures can be taken.

Bibliography. Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Darlington (1931), Franky & Rodríguez (1977), Goehfeld *et al.* (1980), Hilty & Brown (1986), Meyer de Schauensee (1949, 1966), Paynter & Traylor (1981), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Todd & Cumker (1922), Wege & Long (1995).

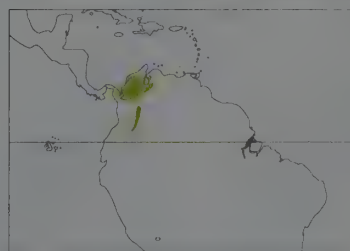
122. Shining-green Hummingbird

Lepidopyga goudoti

French: Colibri de Goudot **German:** Grünkolibri **Spanish:** Colibrí de Goudot
Other common names: Luminous Hummingbird (*luminosa*)

Taxonomy. *Trochilus Goudoti* Bourcier, 1843, Ibagué, Magdalena Valley, Colombia. Race *luminosa* (perhaps including *phaeochroa*) has sometimes been treated as a separate species. Four subspecies recognized.

Subspecies and Distribution.
L. g. luminosa (Lawrence, 1862) - coastal lowlands of N Colombia.
L. g. goudoti (Bourcier, 1843) - middle and upper Magdalena Valley (C Colombia).
L. g. zuliae Cory, 1918 - N & W parts of L Maracaibo basin (extreme NE Colombia and NW Venezuela).
L. g. phaeochroa Todd, 1942 - S & E parts of L Maracaibo basin (NW Venezuela).



Descriptive notes. 9.9-5 cm; male 4.1 g, female 3.7 g. Straightish bill black, with lower mandible mainly pink. Male green above; tail forked, central rectrices bronze-black, lateral rectrices blue-black; most of underparts shining bluish-green, belly whitish, undertail-coverts green with whitish borders. Female resembles male, differing in having broad whitish bases and fringes on underparts, which give a spotty appearance to the lower breast, passing to a nearly pure white belly; undertail-coverts mostly white with green centres, tail less deeply forked than male and less black, more bronzy to greenish. Immature dull bronzy-green below, feathers with prominent greyish-white fringes, passing to greyish-white on belly; duller green above with narrow dusky fringes on feathers of crown and nape. In race *luminosa* male less bluish, more golden green below, more bronzy above, female with less white on belly and undertail-coverts; *zuliae* smaller, crown darker, upperparts less bronzy, undertail-coverts with only narrow whitish borders; *phaeochroa* darker above and bluer on crown, male more bluish-green below.

Habitat. Open, brushy country with scattered trees, hedgerows and scrubby pastures, arid to moist scrub, borders of gallery forest, light woodland, coffee plantations, gardens. From sea-level to 1000 m, occasionally to 1600 m (Colombia); to 800 m in Venezuela.

Food and Feeding. Visits flowers of a variety of shrubs and trees, especially those of legumes like *Inga*, *Calliandra* and *Pithecellobium saman*; sometimes many gather in noisy, quarrelsome assemblages at flowering trees. Along streams, may visit flowers of *Heliconia*, in gardens cultivated *Hibiscus*, etc. Flycatches from exposed perches atop shrubs or small trees, and gleans arthropods from twigs, branches and foliage in tree crowns.

Breeding. Oct-Mar; nest a small cup of pale-coloured plant down and cobwebs, decorated on outside with whitish lichens, on horizontal outer branch of shrub or small tree adjoining open area, 1-1.5 m above ground (*goudoti*). No further information.

Movements. Presumably sedentary; local altitudinal dispersal likely to occur, as perhaps indicated by apparent seasonal changes in abundance in Santa Marta area and S Huila (Colombia).

Status and Conservation. Not globally threatened. CITES II. Locally common over much of range, which has probably expanded in many areas with deforestation. Occurs in Tayrona National Park (NE Colombia). Frequently recorded between San Carlos de Zulía and Encontrados (NW Venezuela).

Bibliography. Cory (1918), Hilty & Brown (1986), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Miller (1947, 1952), Olrog (1968), Peña, M. (1997), Phelps & Phelps (1958), Stotz *et al.* (1996), Todd (1942).



Genus *HYLOCHARIS* Boie, 1831

123. Blue-throated Goldentail

Hylocharis eliciae

French: Saphir d'Elicia **German:** Goldschwanz-Saphirkolibri **Spanish:** Zafiro de Elicia
Other common names: Blue-throated Sapphire

Taxonomy. *Trochilus Eliciae* Bourcier and Mulsant, 1846, no locality = Cobán, Alta Vera Paz, Guatemala.

Two subspecies recognized.

Subspecies and Distribution.

H. e. eliciae (Bourcier & Mulsant, 1846) - SE Mexico and Belize patchily S to S Costa Rica.

H. e. earina Wetmore, 1967 - W Panama, including Coiba I and islands in Bay of Panama, to extreme NW Colombia.



Descriptive notes. 9 cm; male 4.1 g, female 3.6 g. Upper and lower mandible of male bill red with black tip, that of female with culmen and tip black; feet dark grey. Male bronzy-green above, darkest on crown, shading to purplish-bronze on uppertail-coverts and golden bronze on tail; throat and chest purplish-blue, lower breast and sides green, belly greyish-buff. Female like male above, mostly dull buffy below, passing to green laterally; throat and breast spotted with blue. Immature has very little blue, veiled by broad greyish-buff feather fringes, and tail is much duller bronze; upper mandible often mostly greyish to blackish. Race *earina*

is darker above, with the tail duller, more greenish-bronze.

Habitat. In humid areas prefers forest edge, tall second growth, semi-open, light woodland, gardens and hedgerows; in drier areas most numerous in evergreen gallery forest, often entering open areas to feed at flowers. Lowlands locally to 750-1000 m.

Food and Feeding. Visits flowers of shrubs (*Stachytarpheta*, *Hamelia*), large herbs (*Heliconia*, *Renalmia*, *Thalea*), trees (*Inga*, *Pisidium*) and epiphytes like bromeliads in openings and along forest borders, usually near ground but sometimes to lower canopy; flycatches and gleans arthropods from foliage.

Breeding. Dry season, Dec-Apr. During breeding season male sings thin, piercing song of variable phrases of 5-8 notes from perches on horizontal twigs in upper understory or lower canopy, in leks of up to 10. Nest a cup with strongly incurved rim, of fine plant fibres, down and cobwebs, sparsely decorated with bits of lichen. 2-6 m up on horizontal twig in second growth, gallery forest or garden. Clutch size 2. No further information.

Movements. Little information; presumably more or less sedentary except for local wanderings during flowering.

Status and Conservation. Not globally threatened. CITES II. Uncommon to locally common, freely entering open or disturbed areas; has probably increased in some areas, following forest clearance; may disappear locally when vegetation grows too tall and dense.

Bibliography. Binford (1989), Brown & Bowers (1985), Carriker (1910), Dickey & van Rossem (1938), Eisenmann (1952), Feinsinger (1976, 1980), Fogden (1993), Friedmann *et al.* (1950), Hilty & Brown (1986), Howell & Webb (1995a), Johnsgard (1997), Land (1970), Mills & Rogers (1988), Monroe (1968), Olson (1997), Ridgely & Gwynne (1989), Ridgway (1911), Rodríguez (1978), Salaman & Mazariegos (1998b), Skutch (1972), Slud (1960, 1964, 1980), Stiles (1980, 1985b, 1985c), Stiles & Skutch (1989), Stone (1932), Stotz *et al.* (1996), Thurber *et al.* (1987), Vallely & Aversa (1997), Wetmore (1957a, 1968a), Willis & Eisenmann (1979).

124. Rufous-throated Sapphire

Hylocharis sapphirina

French: Saphir à gorge rousse **German:** Rotkehl-Saphirkolibri **Spanish:** Zafiro Gorgirrojo
Other common names: Red-throated Sapphire

Taxonomy. *Trochilus sapphirinus* J. F. Gmelin, 1788, the Guianas.

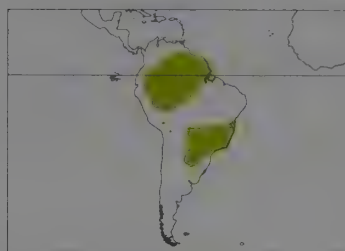
In past, several races were recognized, notably *guianensis* (Guyana) and *brasilensis* (Bahia), but pattern of distinguishing morphological characters is not constant. Monotypic.

Distribution. E Colombia (Vaupés, Amazonas), S Venezuela (Amazonas, Bolívar) and the Guianas to E Ecuador, NE Peru and NW & NC Brazil (Amazonas E to Amapá and Pará); also NE Bolivia (NE Santa Cruz), Paraguay and C & E Brazil (Bahia S to São Paulo) to NE Argentina (Chaco, Formosa, Misiones).

Descriptive notes. 8.4-8.9 cm; male 4.1-4.5 g, female 3.9-4.3 g. Male has medium-sized straight bill, coral red, tipped black; upperparts dark green, uppertail-coverts coppery violet; chin intensely rufous, throat and chest iridescent violet-blue, undertail-coverts chestnut; central rectrices coppery tinged violet, rest chestnut, tipped dusky grey. Female similar to male above, chin pale rufous, underparts greyish with large glittering blue-green discs on throat and chest; undertail coverts buffy, tail as in male, outer rectrices with paler edges. Immature similar to adult female; young male with rich rufous on chin.

Habitat. Forest edge, savanna with scattered bushes and stands of trees, clearings around granite outcrops, coffee plantations, more rarely in open coastal vegetation. Most numerous around 200-500 m, sometimes found at higher elevations up to 1800 m. Forages from low down to medium height on the periphery of vegetation.

Food and Feeding. Nectar of flowering shrubs, small trees, vines and epiphytes, including Leguminosae, Rutaceae, Rubiaceae, Myrtaceae, Loranaceae, Passifloraceae and Bromeliaceae. Usually seen feeding from near the ground to lower strata; in Amazonia, during flowering period,



regular visitor to tree tops. Insects are caught in the air by hawking, spiders gleaned from the surface of leaves or from webs. Male establishes feeding territories, defending them aggressively against intruders.

Breeding. Jul-Jan (the Guianas), Aug-Feb (Brazil). Cup-shaped nest of plant fibre, lined with soft seed-down, sometimes decorated on outer wall with lichen and parts of leaves, is placed on horizontal branch of shrub and tree, protected by overhanging leaves, at 4-6 (3-10) m above the ground. Clutch size 2; incubation 14-16 days, by female; chick blackish with sparse buffy dorsal down; fledging period 22-27 days.

Movements. Sedentary, migratory in parts of SE Brazil. Migration pattern is poorly documented.

Status and Conservation. Not globally threatened. CITES II. A common species in most of range; densities of at least 3-4 pairs/km² in the Voltzberg area of C Surinam. Until recently, presence in Paraguay was considered doubtful, but several sightings during 1990's, e.g. in Caaguazú National Park (Canindeyú). Accepts man-made habitats like coffee plantations, if bordered by natural, semi-open habitats.

Bibliography. Bangs & Penard (1918), Best *et al.* (1997), Brooks, Barnes *et al.* (1993), Brooks, Clay *et al.* (1995), Butler (1979), Canevari *et al.* (1991), Cintra & Yamashta (1990), Contreras *et al.* (1990), Friedmann (1948), Gilliard (1941), Grantsau (1988), Haverschmidt & Mees (1994), Hayes (1995), Hilty & Brown (1986), Lowen, Bartrina, Clay & Tobias (1996), Lowen, Clay *et al.* (1997), Meyer de Schauensee & Phelps (1978), Nores *et al.* (1983), Oniki (1996), Parker *et al.* (1982), de la Peña (1994), Remsen & Traylor (1989), do Rosário (1996), Ruschi (1967a, 1973d, 1981-1982, 1982a, 1986), Rutgers & Norris (1972), Short (1975), Sick (1993, 1997), Snyder (1966), Stotz *et al.* (1996), Tostain *et al.* (1992), Zimmer (1950e).

125. White-chinned Sapphire

Hylocharis cyanus

French: Saphir azuré **German:** Weißkinn-Saphirkolibri **Spanish:** Zafiro Gorgiblancos

Taxonomy. *Trochilus cyanus* Vieillot, 1818, Rio de Janeiro, Brazil.

Species name has alternatively been given as *cyana* or *cyanea*, but original name is a Greek noun, and is not variable. "*H. pyropygia*" is probably a hybrid of present species and *Chlorostilbon aureoventris pucherani*; "*Chlorostilbon hypocyaneus*", known only from two trade skins from Bahia, may be a hybrid of present species with *Chlorostilbon notatus*, or a mutant of that species, or possibly even a valid species. Five subspecies recognized.

Subspecies and Distribution.

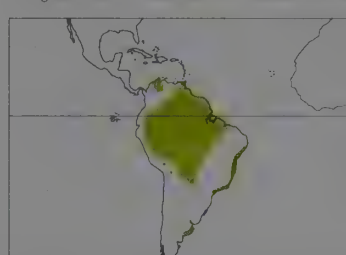
H. c. viridiventris Berlepsch, 1880 - N & E Colombia, W & S Venezuela and the Guianas to N Brazil (to Mato Grosso and Maranhão).

H. c. rostrata Boucard, 1895 - E Peru, NE Bolivia and W Brazil (Mato Grosso); probably E Ecuador.

H. c. conversa Zimmer, 1950 - E Bolivia, N Paraguay and SW Brazil (Mato Grosso do Sul).

H. c. cyanus (Vieillot, 1818) - coastal E Brazil (Pernambuco to Rio de Janeiro).

H. c. griseiventris Grantsau, 1988 - coastal SE Brazil (São Paulo) and NE Argentina (Buenos Aires).



Descriptive notes. 8.9 cm; 3.5 g. Male has bill straight, medium-sized, coral red except for dark tip, or with darker upper mandible: forehead, crown, cheeks, throat brilliant violet-blue, sometimes extending to neck; upperparts golden green, becoming copperish towards rump; chin feathers basally whitish; sides of neck and lower throat bluish; belly and flanks golden green, centre towards belly more greyish; uppertail-coverts deep copperish to purple; undertail-coverts dark bronze-green to copperish or purplish; tail steel blue to bluish-black, median rectrices sometimes deep bronze-green. Female lacks violet-blue head

and throat; upperparts lighter golden green, less contrasting rump, centre of underparts greyish; undertail-coverts white, outer rectrices with grey terminal band. Immature male has head and throat partially bluish-green; belly greyer, undertail-coverts dark greyish. Race *viridiventris* has shorter bill, male has belly darker emerald to bluish-green, and undertail-coverts steel blue to dark purple, whereas female has belly and undertail-coverts partially marked with dark grey; *rostrata* larger in all morphometric characters; *conversa* has longer bill, with belly and undertail-coverts in male paler green to greyish, the latter more strongly margined; male *griseiventris* has crown and throat bluish-green, belly greyish, lower rump generally more coppery to wine red.

Habitat. Inhabits edges of tropical lowland evergreen forests, gallery forests, riparian woodland, clearings with scattered trees, plantations, *capoeiras*; in Amazonia and SE Brazil, also occurs in white sand forests and *restinga*. Ranges from lowlands to sub-montane zone, between 200 and 1000 m; in SE Brazil, close to sea-level.

Food and Feeding. Forages for nectar of various plant species, including Verbenaceae, Loranaceae, Malvaceae, Leguminosae, Myrtaceae, Rutaceae, Convolvulaceae, Rubiaceae, Acanthaceae, Vochysiaceae and Bromeliaceae. Diet also includes spiders, beetles and flies (Diptera). Feeds at all heights from ground to tree tops, sometimes gathering at feeding trees.

Breeding. Almost all year round. Nest cup-like, made of plant fibres, built on a horizontal branch, 1.5-4 m above ground; cobweb and lichen attached to outer wall. Clutch size 2; incubation 14-15 days, by female; fledging at 20-26 days.

Movements. Some local dispersal, especially in eastern parts of range.

Status and Conservation. Not globally threatened. CITES II. Fairly common in more humid areas along forest borders and in riparian woodland; less common in more arid habitats. Accepts man-made habitats, e.g. fruit plantations and parks. Occurs in a considerable number of protected areas, such as Amacayacu National Park (Colombia), Imataca Forest Reserve (Venezuela) and Tambopata Reserve (Peru).

On following pages: 126. Gilded Hummingbird (*Hylocharis chrysura*); 127. Blue-headed Sapphire (*Hylocharis grayi*); 128. Golden-tailed Sapphire (*Chrysura oenone*); 129. White-throated Hummingbird (*Leucochloris albicollis*); 130. White-tailed Goldenthrout (*Polymus guianumbi*); 131. Tepui Goldenthrout (*Polymus milleri*); 132. Green-tailed Goldenthrout (*Polymus theresiae*); 133. Buffy Hummingbird (*Leucippus fallax*); 134. Tumbes Hummingbird (*Leucippus baeri*); 135. Spot-throated Hummingbird (*Leucippus taczanowskii*); 136. Olive-spotted Hummingbird (*Leucippus chlorocercus*); 137. White-bellied Hummingbird (*Leucippus chionogaster*); 138. Green-and-white Hummingbird (*Leucippus viridicauda*); 139. Many-spotted Hummingbird (*Leucippus hypostictus*).

Bibliography. Bangs & Penard (1918), Berlioz (1929a, 1938), Best *et al.* (1997), Bond & Meyer de Schauensee (1943), Butler (1979), Canevari *et al.* (1991), Collar *et al.* (1992), Dabbene (1926), Davis (1993), Donahue (1994), Grantsau (1988), Haverschmidt (1955a), Haverschmidt & Mees (1994), Friedmann (1948), Gilliard (1941), Hilty & Brown (1986), Mayr (1971), Meyer de Schauensee (1949, 1964), Meyer de Schauensee & Phelps (1978), Oniki (1996), de la Peña (1994), Perry *et al.* (1997), Pinto (1938), Remsen & Taylor (1989), Remsen, Taylor & Parkes (1986), Ruschi (1949b, 1981-1982, 1986), Rutgers & Norris (1972), Sánchez (1995), Sick (1993, 1997), Snyder (1966), Stotz *et al.* (1996), Taczanowski (1884), Terborgh *et al.* (1984), Tostain *et al.* (1992), Wege & Long (1995), Weller & Schuchmann (1997), Wetmore & Phelps (1956), Zimmer (1950e).

126. Gilded Hummingbird

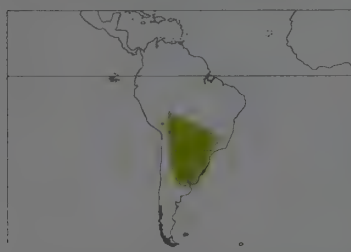
Hylocharis chrysura

French: Saphir à queue d'or **German:** Goldsaphirkolibri **Spanish:** Zafiro Bronceado

Taxonomy. *Trochilus chrysurus* Shaw, 1812, Paraguay.

Some authors recognize a race *platensis* (S Brazil), but size differences and more intense coppery gold on underparts appear to refer to clinal variation. Monotypic.

Distribution. NE & SC Bolivia (Beni, Santa Cruz, Chuquisaca, Tarija), Paraguay and C & SE Brazil (Mato Grosso and Minas Gerais to São Paulo and Rio Grande do Sul) to Uruguay and N Argentina (S to Tucumán, Santiago del Estero, Santa Fe, Buenos Aires).



Descriptive notes. 8-10 cm; 4-4.6 g. Male has medium-sized straight bill, coral red, tipped black; above and below iridescent golden green, tiny white postocular spot, chin pale rufous, rectrices glittering golden bronze. Female similar to male, generally duller, lower belly greyish. Immature similar to adult female, head feathers fringed buff.

Habitat. Gardens, plantations, savannas with scattered bushes and trees, forest edges, from 200 to 1000 m, locally at higher elevations. Forages on the periphery of vegetation from low down to tree tops in clearings. Most numerous between 400 and 800 m.

Food and Feeding. Nectar of flowering native and introduced angiosperms, such as *Inga*, *Vochysia*, *Citrus*, *Eucalyptus*, *Hibiscus*, *Malvaviscus*, *Abutilon* and *Salvia*. Arthropods are caught in the air by hawking or are gleaned from vegetation surface. Collects small spiders from webs.

Breeding. Sept-Feb (Brazil). Small cup-shaped nest is built from seed fibres of *Asclepias*, *Chorisis* and various bromeliads, and cobweb, externally decorated with lichen and pieces of leaf; constructed on thin horizontal branch, rather exposed at height of 4-6 m, occasionally up to 12 m. Clutch size 2; incubation 14-15 days, by female; chick blackish with two dorsal rows of buffy down; fledging period 20-26 days. First breeding in second year.

Movements. Sedentary, migratory in parts of Brazil during Jul and Aug (Mato Grosso). Migration pattern poorly understood.

Status and Conservation. Not globally threatened. CITES II. A very common hummingbird throughout its range; readily takes to man-made habitats such as gardens and plantations. Due to its generalized habitat requirements range expansion can be expected.

Bibliography. Belton (1984), Bond & Meyer de Schauensee (1943), Brooks *et al.* (1993), Canevari *et al.* (1991), Cintra & Yamashita (1990), Contreras *et al.* (1990), Davis (1993), Fiameni (1991), Grantsau (1988), Klimaitis & Moschione (1987), Lowen, Barrina, Clay & Tobias (1996), Lowen, Clay *et al.* (1995), Motaldo (1984), Naumburg (1930), Navas & Bo (1993), Olog (1963c), Oniki (1996), de la Peña (1994), Pinto (1932), Pinto & de Camargo (1955), Remsen & Taylor (1989), Remsen, Taylor & Parkes (1986), do Rosário (1996), Ruschi (1973d, 1981-1982, 1982a, 1986), Saibene *et al.* (1996), Short (1975), Sick (1993, 1997), Stotz *et al.* (1996), Tobias *et al.* (1993), Wetmore (1926).

127. Blue-headed Sapphire

Hylocharis grayi

French: Saphir ulysse **German:** Blaukopf-Saphirkolibri **Spanish:** Zafiro Cabeciazul
Other common names: Gray's/Puritan Sapphire

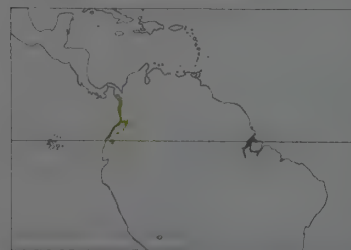
Taxonomy. *Trochilus Grayi* DeLattre & Bourcier, 1846, Popayán, Colombia.

Formerly segregated in monospecific genus *Eucephala*. Races are so different in coloration, measurements and ecology that they should perhaps be considered separate species, probably forming a superspecies. Two subspecies currently recognized.

Subspecies and Distribution.

H. h. humboldtii (Bourcier & Mulsant, 1852) - extreme SE Panama to NW Ecuador.

H. h. grayi (DeLattre & Bourcier, 1846) - W Colombia and N Ecuador.



Descriptive notes. 10-11 cm; male 6.5-6.8 g, female 6.1-6.4 g. Bill of male mostly coral-red with black tip; upper mandible of female black tinged red basally, lower pinkish with black tip; feet blackish. Male of nominate has upper throat, face and crown deep glittering blue, nape dark blue-green, rest of underparts metallic green, forked tail dark steel blue; lower throat, breast and upper belly glittering emerald green, a small area of greyish-white on lower belly, undertail-coverts metallic green edged with dark grey. Female metallic green to bronze-green above; tail dark bronze-green basally, blue-black distally, outer rectrices

tipped greyish-white; below mostly greyish-white to dull white, sides of throat and breast extensively bronze-green, some bright green flecking across lower throat. Immature male lacks glittering blue or green on head and underparts; face and crown dull bluish-green, throat and breast bronzy-green, belly greyish-white, tail dusky grey at tip; immature female duller, more bronzy above and below. Race *humboldtii* has bill shorter on average, wings and tail longer. In male *humboldtii*, deep blue restricted to forehead and centre of throat, shading through blue-green to glittering green on chest, sides of neck, and malar area; sides green, most of belly and undertail-coverts white, the white typically extending forwards as a broad median stripe that ends abruptly on lower breast; crown dark dull blue-green, rest of upperparts metallic green to bronze-green, tail dark metallic green to blue, the outer rectrices more or less tipped dusky grey and narrow. Female

humboldtii averages much whiter below than nominate, heavily flecked with bright green on sides of throat and breast; crown bluer; tail metallic green to bronze-green, shading to dusky grey distally on lateral rectrices, which are more or less tipped pale grey. Immature male *humboldtii* more extensively white below than adults; medial throat and breast greyish flecked bronze, passing to bronze-green laterally; crown and face dull dark bluish-green.

Habitat. Nominat race occurs in dry scrub and woodland edges in dry, rain-shadow valleys of Pacific slope, also in cultivated areas, light woodland and forest borders in Andes, mostly at c. 500-2000, rarely 2600 m; *humboldtii* found along Pacific coast in mangroves and adjacent wet second growth, forest edges, mostly below 50 m, being commonest in areas where Pacific mangrove (*Pelliciera rhizophorae*) abundant. Few records of either race from intervening areas.

Food and Feeding. Nominat visits flowers of a variety of shrubs and trees, sometimes many gather in crowns of flowering trees where notably aggressive, sometimes defending feeding territories. Favourite flower of *humboldtii* is that of *Pelliciera*, but at times (perhaps seasonally) visits flowers of various shrubs, trees and large herbs like *Heliconia* in areas adjacent to mangroves. Both forms hawk flying insects from perches adjoining open areas or water, and glean small arthropods off foliage.

Breeding. Birds in breeding condition recorded Nov-Apr (*grayi*), Jan-May (*humboldtii*); nest undescribed. No further information.

Movements. Marked seasonal movements reported for *grayi*, which is erratic in most areas, but details lacking; no information for *humboldtii*.

Status and Conservation. Not globally threatened. CITES II. Cutting of mangroves for shrimp farming or firewood has doubtless resulted in much habitat loss for race *humboldtii* in some areas. Race *grayi* seems able to use more or less extensively altered, open or cultivated areas, though in Colombia, probably no longer occurs regularly in much of Cauca Valley, which has been converted to extensive rice and sunflower plantations; also, in Patía Valley, now found mostly in scattered remnants of natural vegetation.

Bibliography. Anon. (1998a), Best *et al.* (1997), Butler (1979), Chapman (1917, 1926), Fjeldsá & Krabbe (1990), Haffer (1986), Hilty & Brown (1986), Meyer de Schauensee (1949, 1982), Miller (1963), Negret (1992), Olog (1968), Ralph & Chaplins (1973), Ridgely & Gwynne (1989), Rutgers & Norris (1972), Stotz *et al.* (1996), Wetmore (1968a).

Genus *CHRYSURONIA* Bonaparte, 1850

128. Golden-tailed Sapphire

Chrysuronia oenone

French: Saphir oenone **German:** Bronzeschwanz-Saphirkolibri **Spanish:** Zafiro Colidorado

Taxonomy. *Ornismya aenone* Lesson, 1832, Trinidad; probably error = north-east Venezuela.

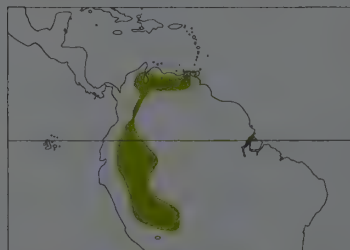
Monotypic genus, sometimes merged into *Hylocharis* because of similarity in plumage, but lacks swollen base of bill and enlarged nasal operculum of that genus. Proposed type locality of Trinidad seems unlikely, as there are apparently no definite records with specific localities, and the species is not mentioned in any work on Trinidad birds during present century. Race *alleni* may not be adequately separable from *josephinae*. Several other races proposed: *longirostris* from E Colombia differs from nominate only in average bill length; *azurea*, supposedly from W Ecuador but no definite records thence (in fact, probably from E Ecuador), has characters of a subadult male of *oenone*; *peruviana* doubtfully distinct from *josephinae*; and *intermedia* of upper Amazonia probably of hybrid origin. "Thalurania lerchii", known from Bogotá trade skins, is apparently a hybrid between present species and *Thalurania furcata*. Three subspecies currently recognized.

Subspecies and Distribution.

C. o. oenone (Lesson, 1832) - N & E Venezuela, E Colombia, E Ecuador, extreme NE Peru and adjacent extreme W Brazil.

C. o. josephinae (Bourcier & Mulsant, 1848) - most of E Peru.

C. o. alleni (Elliot, 1888) - N Bolivia.



Descriptive notes. 9.5-10 cm; male 4-7 g, female 4-3 g. Upper mandible black, lower red with black tip. Male has entire head and throat violet-blue, breast glittering green passing to bronzy-green on belly, undertail-coverts bronze edged with whitish; back bright green, shading through bronze-green to brilliant coppery upperside-coverts and copper-bronze tail. Female has crown blue, shading to green on back and copper-bronze on upperside-coverts and tail; below mostly whitish, heavily flecked with blue-green on sides of throat and neck, and green on sides and across chest, bronze-green on flanks; undertail-coverts with bronzy

centres. Immature male has crown dull green, throat dusky grey with dull buffy feather fringes and chest duller green; the first generation of blue feathers on the head and throat are more blue, less violet than in adult male; immature female has the green spotting below duller and more bronzy, less bluish than in adults. In race *josephinae*, male has throat mostly green, rump green contrasting more with coppery tail-coverts; *alleni* has no blue on throat and little or none on malar area, with rump more or less coppery in both sexes.

Habitat. Humid forest, especially at gaps and along edges, old second growth, gallery forest, semi-open areas like shaded cacao and coffee plantations, gardens and deciduous forest (Venezuela); mainly in foothills and adjacent lowlands, from sea-level to 1500 m (Colombia & Venezuela).

Food and Feeding. Visits mostly flowering trees (*Erythrina*, *Inga*) and shrubs (*Aphelandra*, *Palicourea*) for nectar; many may gather in quarrelsome assemblages at flowering trees, female more often trap-lines dispersed flowers in forest; male occasionally defends territories at flowers when more aggressive species like *Thalurania furcata* are absent; flycatches from perches at forest edge or gaps, and gleans arthropods from foliage.

Breeding. Birds in breeding condition Jun-Nov in E Colombia. During breeding season males usually in leks of 5-10, occasionally solitary. No further information.

Movements. Little information available; movements across Portachuelo Pass reported at Rancho Grande, Venezuela; presumably moves locally in response to shifts in flowering.

Status and Conservation. Not globally threatened. CITES II. Fairly common, at least locally, in foothill areas of Colombia and Venezuela, but relatively rare in Amazonian lowlands far from the Andes. In Colombia, known to use disturbed and fragmented forests.

Bibliography. Best *et al.* (1997), Blake (1962), Bloch *et al.* (1991), Bond & Meyer de Schauensee (1943), Butler (1979), Cotton (1998a), Donahue (1994), Grantsau (1988), Hilty & Brown (1986), Meyer de Schauensee & Phelps (1978), Mobbs (1972c), Parker *et al.* (1982), Remsen & Traylor (1989), Ruschi (1953a, 1986), Salaman & Mazariegos (1998a, 1998b), Schäfer & Phelps (1954), Sick (1993, 1997), Stotz *et al.* (1996), Terborgh *et al.* (1984), Wetmore (1939), Williams & Tobias (1994), Zimmer (1930, 1950c).

Genus *LEUCOCHLORIS* Reichenbach, 1854

129. White-throated Hummingbird

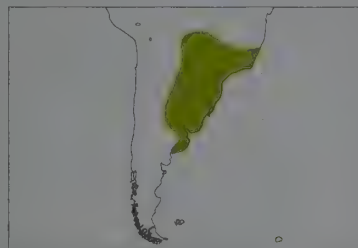
Leucochloris albicollis

French: Colibri à gorge blanche **German:** Weißkehlkolibri **Spanish:** Colibri Gargantilla
Other common names: Brazilian White-throated Hummingbird

Taxonomy. *Trochilus albicollis* Vieillot, 1818, São Paulo, Brazil.

"*L. malvina*", known only by type specimen from Rio de Janeiro, may be hybrid of present species and *Chlorostilbon aureoventris*. Monotypic.

Distribution. E Bolivia, E Paraguay, N Argentina and SE Brazil (Minas Gerais to Rio Grande do Sul); possibly also N Uruguay.



Descriptive notes. 10-11.5 cm; male 5.0 g, female 4.5 g. Male has bill straight, medium-sized, upper mandible blackish, lower flesh red with dark tip; upperparts golden to bronze-green; chin and throat brilliant green with white feather margins; cheeks and breast brilliant green to golden green; throat patch oval, white; flanks and belly golden to bronze-green; centre of belly white; undertail-coverts white, basally with bronze-green to brownish centres; uppertail-coverts and inner rectrices golden to brilliant green, lateral rectrices becoming blackish-green with white terminal bands. Female similar to male, but less glittering in plumage.

Immature has underparts more greyish-brown, less white; rectrices tipped brownish.

Habitat. Found along forest edges and in marshy habitats; also in open areas with scrub, or parks and gardens; from near sea-level to 1000 m.

Food and Feeding. Forages for nectar at various native and introduced plant species; often seen at Leguminosae (*Dahlstedtia*, *Inga*, *Dioclea*), Apocynaceae (*Mandevilla*), Acanthaceae (*Mendoncia*), Rubiaceae (*Manettia*), Lobeliaceae (*Lobelia*), Heliconiaceae, Agavaceae (*Phormium*), Bromeliaceae (*Nidularium*, *Vriesea*); also visits introduced plants, including *Citrus*, *Malvaviscus*, *Abutilon* and *Salvia*. Insects are caught by hawking.

Breeding. Oct-Mar. Nest cup-shaped, and consists of plant down and moss, externally decorated with lichens fixed with cobweb; built on horizontal branches of smaller trees and bushes. Clutch size 2; incubation 14 days, by female; fledging period 20-25 days.

Movements. Some local dispersal.

Status and Conservation. Not globally threatened. CITES II. Especially common in SE parts of range where widely adapted to man-made habitats. Range extension at SW limits of distribution; recent spread has been proven for Argentina, where now regularly occurs as breeder in provinces of Buenos Aires, Córdoba and Mar del Plata; additional records from E Bolivia. Current status and southern limits in Uruguay remain unclear.

Bibliography. de Almeida & Ruschi (1976), Belton (1984), Berlioz (1934, 1938), Berry (1989), Bo & Darrieu (1988), Brooks *et al.* (1993), Canevari *et al.* (1991), Contreras & Contreras (1990), Contreras *et al.* (1990), De Lucca (1990), Grantsau (1988), Hayes (1995), Lowen, Bartrina, Clay & Tobias (1996), Maragliano (1994), Montaldo (1984, 1995a), Narosky (1983), Narosky & Yzurietta (1993), Núñez (1992), Olrog (1963a), Oniki (1996), de la Peña (1994), Pereyra (1965), Pinto (1938, 1978), Roitman & Neumann (1995), do Rosário (1996), Ruschi (1949a, 1981-1982, 1982a, 1986), Rutgers & Norris (1972), Saibene *et al.* (1996), Sazima, I. *et al.* (1996), Sazima, M. *et al.* (1994), Sick (1993, 1997), Simon & Hellmayr (1908), Snow & Snow (1986), Snow & Teixeira (1982), Storer (1989), Stotz *et al.* (1996), Todd (1938), Wittmann (1982).

Genus *POLYTMUS* Brisson, 1760

130. White-tailed Goldenthrout

Polytmus guainumbi

French: Colibri guainumbi **German:** Bronzerücken-Glanzkehlchen **Spanish:** Colibri Guainumbi
Other common names: White-tailed Hummingbird(?)

Taxonomy. *Trochilus guainumbi* Pallas, 1764, Cape of Good Hope; error = Surinam.

Genus probably constitutes an old Guianan and C Brazilian element with close morphological and behavioural affinities with *Leucochloris* and *Leucippus*. In past, genus was considered monospecific, comprising present species only. Forms a superspecies with *P. milleri*. Name *andinus* was thought to be preoccupied and this taxon was thus renamed "*doctus*", but renaming unjustified. Three subspecies recognized.

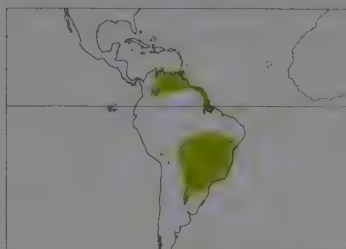
Subspecies and Distribution.

P. g. andinus Simon, 1921 - E Colombia (S to Meta and Vichada).

P. g. guainumbi (Pallas, 1764) - Venezuela and Trinidad to the Guianas and N Brazil.

P. g. thaumantias (Linnaeus, 1766) - E Bolivia, E Paraguay and C & E Brazil (S Maranhão and Bahia to Mato Grosso do Sul, São Paulo and N Paraná) to NE Argentina.

Descriptive notes. 9.7-10 cm (including bill of 2.5 cm); 4.5-5 g. Male has long bill, decurved, upper mandible dull reddish to black, lower reddish, tipped black; upperparts shining golden to bronzy-green, dusky grey eye patch bordered above and below by long white streak; underparts



iridescent golden green; tail rounded, long, green, tipped white, broad white edges on outer 3 rectrices. Female similar to male but with buffy facial streaks; chin whitish, rest of underparts buff, throat and breast spotted green. Immature like adult female, head feathers fringed buff. Race *andinus* has more white on inner rectrices; *thaumantias* similar to nominate but bill shorter, upperparts reddish-golden, less white on outer tail feathers.

Habitat. Waterlogged grassland, shrubby savanna, *cerrado*, freshwater swamps, from sea-level to 600 m. Forages very close to ground; solitary.

Food and Feeding. Nectar of flowering garden plants such as *Lagerstroemia*, low-growing shrubs like *Russelia*, clumps of *Heliconia*, Leguminosae, Malvaceae, or Rubiaceae. Insects are caught in the air by hawking, spiders are gleaned from the surfaces of vegetation.

Breeding. Mar-Aug (Trinidad, Surinam), Feb-Apr and Jul-Sept (French Guiana), Oct-Nov (Venezuela), Oct-Mar (Brazil). Nest is cone-shaped cup of plant down (usually from *Typha*) decorated with lichen or seed, built in fork of small shrub, exposed, c. 0.5-1 m above ground, often over water; nests sometimes in close vicinity to each other. Clutch size 2; incubation 14-15 days, by female; chick black with sparse buffy dorsal down; fledging period 20-22 days.

Movements. Mostly sedentary; in Trinidad seasonal dispersal following reproduction.

Status and Conservation. Not globally threatened. CITES II. Common to locally abundant throughout most of range; rather uncommon and local on Trinidad. Habitats in many parts of range are not seriously threatened. Regularly recorded in Das Emas National Park, Goiás, and also in Pantanal of Mato Grosso (Brazil).

Bibliography. Baldo *et al.* (1995), Canevari *et al.* (1991), Cintra & Yamashita (1990), Contreras & Contreras (1990), Contreras *et al.* (1990), Costa & Bornschein (1995), Davis (1993), Esteban (1947), French (1991), Friedmann & Smith (1950), Gilliard (1941), Grantsau (1988), Hartert (1899b), Haverschmidt & Mees (1994), Hayes (1995), Herklots (1961), Hilty & Brown (1986), Lowen, Bartrina, Clay & Tobias (1996), Meyer de Schauensee & Phelps (1978), Oniki (1996), de la Peña (1994), Perry (1994), Remsen & Traylor (1989), Remsen, Traylor & Parkes (1986), Rovira & Beltzer (1992), Ruschi (1981-1982, 1982a, 1986), Saibene *et al.* (1996), Salaman & Mazariegos (1998a), Short (1971, 1975), Sick (1993, 1997), Snyder (1966), Stotz *et al.* (1996), Thomas, B.T. (1979), Todd (1942), Tostain *et al.* (1992), Zimmer (1950f).

131. Tepui Goldenthrout

Polytmus milleri

French: Colibri des tépuis **German:** Tepuiglänzkehlchen **Spanish:** Colibri de Tepui

Taxonomy. *Waldronia milleri* Chapman, 1929, Mount Duida, 4700 feet [c. 1450 m], Venezuela.

Genus probably constitutes an old Guianan and C Brazilian element with close morphological and behavioural affinities with *Leucochloris* and *Leucippus*. Formerly separated in monotypic genus *Waldronia*. Forms a superspecies with *P. guainumbi*. Monotypic.

Distribution. Table mountains in Venezuela (Duida, Jauna, Auyán Tepui, Parítepui, Roraima and Serra de Pacaraima) and N Brazil (Roraima).



Descriptive notes. 11-12 cm (including bill of 2.5 cm); male 5.6-1 g, female 4.1-4.8 g. Male similar to *P. guainumbi* but no white at eye; long, slightly decurved bill is black; upperparts bronzy-green; below glittering green; central pair of rectrices bronze-green above, iridescent green below, all other tail feathers green, broadly white at base, more narrowly tipped white. Female like male but smaller; mainly dull white below, heavily dotted golden green, densest on breast; more lightly coloured underneath. Immature like adult but with buffy fringes to head feathers.

Habitat. Cloudforest edge, scrub with scattered trees at 1300-2200 m. Forages low down at periphery of vegetation; solitary.

Food and Feeding. Nectar of flowering terrestrial Bromeliaceae, Gesneriaceae, Ericaceae, or Myrtaceae. Insects are caught in the air by hawking, spiders are gleaned from rock cavities and vegetation.

Breeding. May-Jun. Cone-shaped nest, lined with fine plant fibre, decorated with lichen and fragments of leaf, is saddled in fork of shrub, rather exposed, at 0.5-1 m above ground. Clutch size 2; incubation 15-16 days, by female.

Movements. Sedentary, with some altitudinal dispersal after breeding.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Tepuis EBA. A little-known tepui endemic. Uncommon to locally common along cloudforest ridges of table mountains. Frequently recorded in La Escalera area, in E Bolívar (Venezuela).

Bibliography. Forrester (1993), Gilliard (1941), Grantsau (1988), Mayr & Phelps (1967), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Olrog (1968), Renjifo *et al.* (1997), Ruschi (1981-1982, 1982a, 1986), Sick (1993, 1997), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Zimmer (1950f).

132. Green-tailed Goldenthrout

Polytmus theresiae

French: Colibri tout-vert **German:** Grünschwanz-Glanzkehlchen **Spanish:** Colibri de Teresa
Other common names: Green Goldenthrout

Taxonomy. *Ornismya theresiae*, Da Silva Maia, 1843, Pará, Brazil.

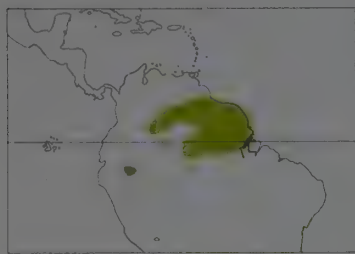
Genus probably constitutes an old Guianan and C Brazilian element with close morphological and behavioural affinities with *Leucochloris* and *Leucippus*. Formerly separated in monospecific genus *Smaragditus*. Two subspecies recognized.

Subspecies and Distribution.

P. t. theresiae (Da Silva Maia, 1843) - the Guianas and NC Brazil (Amazonas, Pará, Amapá).

P. t. leucorrhous P.L. Selater & Salvin, 1867 - E Colombia and S Venezuela (Bolívar, Amazonas) to NW Brazil (R Negro) and NE Peru (Loreto).

Descriptive notes. 8.9-9.9 cm (including bill 2.5 cm); 3.5-3.9 g. Male has long bill, slightly decurved, upper mandible black, lower flesh-coloured, tipped black; upperparts and underparts shining green,



small white postocular spot; tail roundish, central rectrices green, others green, basally white. Female similar to male, smaller; throat and breast whitish, thickly spotted with green; outer rectrices with narrow white tips. Immature like adult female but with head feathers fringed buff. Race *leucorrhous* generally very similar but vent and undertail-coverts extensively white with green discs.

Habitat. Forest edge and sandy savanna with scattered stands of bushes and small trees from 100 to 300 m altitude.

Food and Feeding. Nectar of flowering Melastomataceae. Arthropods are gleaned

from leaves or caught in the air by hawking. Male occasionally occupies feeding territories; usually both sexes forage by trap-lining.

Breeding. Mar-Apr and Aug-Oct (the Guianas), Oct-Nov (Venezuela), Nov-Mar (Brazil). Small cup-shaped nest of fine, buff-coloured plant fibre and cobweb is built, rather visibly, in fork of low shrub, often Melastomataceae such as *Rhynchanthera* or *Tibouchina*. Clutch size 2; incubation 14 days, by female; chick black with two rows of buff dorsal down; fledging period 20 days, sometimes up to 28 days.

Movements. Sedentary, but some wandering is known in Surinam, where species may occur at coastal mangrove areas in Jan-Feb.

Status and Conservation. Not globally threatened. CITES II. A common and locally very abundant savanna bird at table mountain borders in La Gran Sabana, S Venezuela, and similar habitats in Surinam and French Guiana.

Bibliography. Best *et al.* (1997), Butler (1979), Chubb (1916), Friedmann (1948), Grantsau (1988), Haverschmidt & Mees (1994), Hilty & Brown (1986), Meyer de Schauensee & Phelps (1978), Parker *et al.* (1982), Ruschi (1953a, 1981-1982, 1982a, 1986), Sick (1993, 1997), Snyder (1966), Stotz *et al.* (1996), Thomas, B.T. (1979), Tostain *et al.* (1992), Zimmer (1950f).

Genus *LEUCIPPUS* Bonaparte, 1850

133. Buffy Hummingbird

Leucippus fallax

French: Colibri trompeur

German: Zimbrustkolibri

Spanish: Colibrí Ante

Taxonomy. *Trochilus fallax* Bourcier, 1843, Caracas, Venezuela.

Proposed races *cervina* (NE Colombia), *occidentalis* (NW Venezuela) and *richmondi* (Margarita I and Tortuga I, off NC Venezuela) are doubtfully distinct; differences apparently represent individual variation. Monotypic.

Distribution. Coastal area of Colombia and Venezuela and adjacent offshore islands.



Descriptive notes. 8.5-9 cm. Male has straight bill, upper mandible black, lower fleshy tipped black; upperparts faded dull green, postocular spot white; underparts pale cinnamon-buff, lower belly white, undertail-coverts white; tail slightly rounded, dull green with dusky grey subterminal bar, tipped white. Much individual variation in overall tone of coloration, from paler to brighter birds, in past forming basis of proposed races. Female similar to male, but tends to be generally duller. Immature resembles adult female.

Habitat. Xeric areas, arid thorny scrub and mangroves, from sea-level up to 550 m. For-

ages at low to medium level in bushes and trees.

Food and Feeding. Feeds on nectar of flowering *Agave*, *Hibiscus*, *Lemairocereus*, *Melocactus* and *Opuntia*. Has been reported to feed on juice of fruits of *Lemairocereus*. Catches insects in the air by hawking.

Breeding. Nests have been found in May and Nov, suggesting breeding period in the rainy season (May-Nov/Dec); one fledgling fed by female in early Dec (Venezuela). Cup-shaped nest is small, made from soft fibres of *Gossypium arboreum* fruits, exterior is decorated with bark, pieces of leaves and lichens; saddled on horizontal branch or in fork of twig, 1.5-2 m above ground. Clutch size 2; no data on incubation and fledging periods available.

Movements. Some seasonal dispersal; during dry season (Dec-Apr) is more abundant in thorn forest and almost absent in the more arid thorn scrubs.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Caribbean Colombia and Venezuela EBA. Common, and most abundant hummingbird species within its rather specialized habitat. Accepts man-made environments like flowering gardens, and is common in suburbs. Parts of habitat are under threat of destruction resulting from rapidly growing tourism in Venezuela; range is partly protected by several national parks, e.g. Henri Pittier National Park (Venezuela).

Bibliography. Berlepsch (1908), Cory (1915), Deignan (1961), Friedmann & Smith (1955), Harrison (1982), Hilty (1994), Hilty & Brown (1986), McNeil & Rodríguez (1985), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Olrog (1968), Phelps & Phelps (1949a, 1958), Robinson & Richmond (1895), Salaman & Mazariegos (1998a), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Todd & Carriger (1922).

134. Tumbes Hummingbird

Leucippus baeri

French: Colibri de Tumbes

German: Baerkolibri

Spanish: Colibrí de Tumbés

Taxonomy. *Leucippus Baeri* Simon, 1901, Tumbes, Peru. Monotypic.

Distribution. Extreme SW Ecuador (Loja) and extreme NW Peru (Tumbes, Piura, Lambayeque).



Descriptive notes. 9-10 cm; 4.3-4.6 g. Male has bill straight or slightly decurved, entirely blackish; upperparts light golden green, feathers bordered dark grey; underparts pale cinnamon to greyish-coloured, becoming whitish towards belly; tail light green, inner rectrices with bronzy tips, outer rectrices with dusky grey subterminal band and whitish terminal patch. Female has more greyish tips in outer rectrices. Immature plumage unknown.

Habitat. Desert scrub, dry forest of the littoral, arid tropical zone, also deciduous forest and scrub; from sea-level to 1300 m.

Food and Feeding. Forages for nectar in xerophytic vegetation, for instance at Cactaceae; diet includes small insects.

Breeding. No information available.

Movements. Presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Tumbesian Region EBA. Fairly common inhabitant of the littoral region. However, considering the extremely limited range and unknown population size, species is potentially threatened by habitat alterations. Precise limits of range remain uncertain.

Bibliography. Best & Clarke (1991), Best & Kessler (1995), Best *et al.* (1997), Cook (1996), Cory (1918), Greenway (1978), Meyer de Schauensee (1966, 1982), Olrog (1968), Parker *et al.* (1982), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Williams & Tobias (1994), Zimmer (1950f).

135. Spot-throated Hummingbird

Leucippus taczanowskii

French: Colibri de Taczanowski

German: Taczanowskikolibri

Spanish: Colibrí de Taczanowski

Other common names: Taczanowski's White-throat

Taxonomy. *Thaumasius taczanowskii* P. L. Sclater, 1879, Guajungo, Cajamarca, Peru.

Formerly placed in monospecific genus *Thaumasius*, or with *L. chlorocercus* and sometimes *L. hypostictus* in *Talaphorus*. Proposed race *fractus*, from Huancabamba (N Peru), doubtfully distinct. Monotypic.

Distribution. W slope of C Andes in N & C Peru.



Descriptive notes. 11.5-12.5 cm; male 7-7 g, female 6-9 g. Male has bill slightly decurved, long, almost blackish; bronze crown; upperparts greyish golden-green to bronze-green; uppertail-coverts bronze, fringed greyish; underparts light drab grey, with glittering golden green spots on chin, throat and flanks; undertail-coverts with light brown centres, whitish edges; inner rectrices entirely greyish-green to bronze-green, outer rectrices becoming more greyish with subterminal bronze patch. Female very similar to male. Immature plumage unknown.

Habitat. Inhabits dry forest and desert scrub with Cactaceae, and plantations. Regularly found between 350 and 1000 m, occasionally up to 3000 m.

Food and Feeding. Nectar of various native and introduced plants such as *Agave* and banana (*Musa*). Insects are caught in the air by hawking.

Breeding. No information available.

Movements. No information available.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Marañón Valley EBA and Peruvian High Andes EBA. Considered to be locally fairly common within the arid tropical zone. Occurs in the Trujillo-Chiclayo area.

Bibliography. Bangs & Noble (1918), Cory (1918), Davies *et al.* (1994, 1997), Koepcke (1961), Meyer de Schauensee (1982), Moynihan (1979), Olrog (1968), Parker *et al.* (1982), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Taczanowski (1884), Zimmer (1950f).

136. Olive-spotted Hummingbird

Leucippus chlorocercus

French: Colibri à queue verte

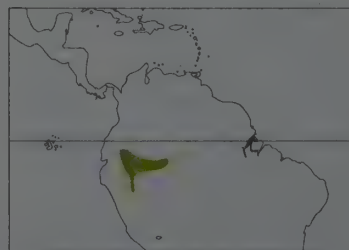
German: Fleckenkolibri

Spanish: Colibrí Blanquioliva

Taxonomy. *Leucippus chlorocercus* Gould, 1866, upper River Ucayali, eastern Peru.

Formerly placed in genus *Talaphorus*, alone or with *L. taczanowskii*, sometimes also with *L. hypostictus*. Monotypic.

Distribution. Extreme SE Colombia, E Ecuador, NE Peru and extreme NW Brazil.



Descriptive notes. 12 cm; 6.0 g. Male has straight, medium-sized, blackish bill; crown and neck bronze; rest of upperparts greyish-green to bronze-green; underparts whitish; throat with olive green, at certain light angles glittering golden green spots; tail pale greyish-green to olive green; greyish tips to median rectrices, extending to the outer webs in lateral rectrices; dark subterminal bar in outer rectrices. Female similar to male, bill slightly longer. Immature with more greyish-brown on underparts.

Habitat. Evergreen tropical forests and glades of upper Amazon Basin and tributaries; occurs

below 150 m.

Food and Feeding. Forages for nectar at species of diverse plant families, including Leguminosae, Lorantaceae, Vochysiaceae, Bromeliaceae, Rutaceae, Bombacaceae, Malvaceae, Rubiaceae, Myrtaceae, Passifloraceae. Gleans insects from leaf surfaces.

Breeding. Breeding season unknown. Nest cup-shaped, made of soft plant material, fibres, cobweb, externally decorated with lichen; placed on horizontal branch at height of 2-10 m. Clutch size 2; incubation 14-15 days, by female; fledging at 20 days.

Movements. Some local dispersal.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Upper Amazon-Napo Lowlands EBA. Fairly common to rare resident along riversides. Potentially threatened by deforestation, caused for example by burning. Range limits unclear; current distribution in Ecuador and NW Brazil needs further clarification.

Bibliography. Anon. (1972), Best *et al.* (1997), Butler (1979), Forrester (1993), Grantsau (1988), Hilty & Brown (1986), Meyer de Schauensee (1982), Olrog (1968), Parker *et al.* (1982), Romero (1978), Ruschi (1986), Sclater & Salvin (1866), Sick (1993, 1997), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Taczanowski (1884), Zimmer (1950f).

137. White-bellied Hummingbird

Leucippus chionogaster

French: Ariane à ventre blanc **German:** Weißbauchamazilie **Spanish:** Colibrí Ventrínveo

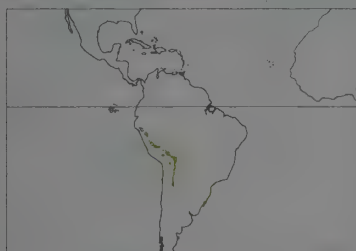
Taxonomy. *Trochilus chionogaster* Tschudi, 1845, Peru.

Has been included by most modern taxonomists in genus *Amazilia*, but separation from *Leucippus* cannot be maintained, for reasons of morphology, behaviour and biogeography. In past, alternatively placed in genus *Chionogaster*, along with *L. viridicauda*; sympatric with that species in Urubamba Valley (C Peru), but hybridization not yet demonstrated. Formerly listed as *L. pallidus*. Proposed race *longirostris*, described from Salta, Argentina, doubtfully distinct from *hypoleucus*; differences in morphometry (e.g. bill length) and plumage characters of subpopulation concerned appear not to be significant. "*L. nigriristris*" generally considered synonym of present species, though may be better considered unidentifiable. Two subspecies recognized.

Subspecies and Distribution.

L. c. chionogaster (Tschudi, 1844) - N & C Peru.

L. c. hypoleucus (Gould, 1846) - SE Peru, Bolivia and NW Argentina; possibly also EC Brazil (Mato Grosso) and Paraguay.



Descriptive notes. 9-12 cm; male 5-5 g, female 4-5 g. Male has straight, medium-sized bill, upper mandible blackish, lower reddish with dark tip; upperparts, sides of chest and flanks golden to light brilliant green; underparts centrally whitish, sparsely spotted golden green on chin and sides of throat; undertail-coverts whitish, sometimes basally golden green; inner rectrices greyish brilliant green to golden green; outer rectrices with white coloration extending to inner webs. Female has chin and throat lightly cream-coloured, the latter more heavily spotted green. Immature shows cream-coloured parts extending to belly;

generally more greener below. Race *hypoleucus* has generally more cream-coloured tinge to underparts; extension of white parts of outermost rectrices covers only the basal half of inner webs; female with characteristic white terminal patch in outer three rectrices.

Habitat. Inhabits forest edges, second growth, wooded ravines, shrub, *cerrado*, plantations, gardens; prefers fairly dry, bushy areas of with Cactaceae, *Agave*, groves of *Alnus* or *Eucalyptus*. Mainly found in the sub-montane, humid temperate to upper tropical zone between 450 and 2000 m; occasionally up to 2800 m.

Food and Feeding. Feeds on nectar of various plants of different families, such as Leguminosae, Vochysiaceae, Malvaceae, Lorantaceae, Bignoniaceae, Bombacaceae, Passifloraceae, Musaceae. Diet also includes small insects.

Breeding. Jan-Mar. Nest cup-shaped, made of plant wool and moss, covered with lichens; located in shrubs or on lower branches of small trees, 2-5 m above ground. Clutch size 2; incubation 14-15 days, by female; fledging period 19-22 days.

Movements. Sedentary; some local dispersal in Argentina.

Status and Conservation. Not globally threatened. CITES II. Locally common. May suffer from destruction of habitat by burning or grazing, especially in areas of relatively arid, open to semi-open vegetation, as in Gran Chaco of SE Bolivia and N Argentina. Common in Calilegua National Park, Jujuy (Argentina).

Bibliography. Babarskas *et al.* (1995), Bond & Meyer de Schauensee (1943), Canevari *et al.* (1991), Contreras *et al.* (1990), Cory (1918), Esteban (1953), Fjeldså & Krabbe (1990), Flores & Capriles (1998), Forrester (1993), Grantsau (1988), Meyer de Schauensee (1982), Narosky & Yzurieta (1993), Parker *et al.* (1982), de la Peña (1994), Pinto (1938), Remsen & Traylor (1989), Ruschi (1986), Schmitt *et al.* (1997), Short (1975), Sick (1993, 1997), Stotz *et al.* (1996), Taczanowski (1884), Wetmore (1926), Zimmer (1930, 1950f).

138. Green-and-white Hummingbird

Leucippus viridicauda

French: Ariane du Pérou **German:** Grünweißamazilie **Spanish:** Colibrí Blanquiverde

Taxonomy. *Leucippus viridicauda* Berlepsch, 1883, Huyro, 4800 feet [c. 1470 m], Peru. Often placed in genus *Amazilia*, but separation from *Leucippus* cannot be maintained, for reasons of morphology, behaviour and biogeography. In past, alternatively placed in genus *Chionogaster*, along with *L. chionogaster*; sympatric with that species in Urubamba Valley (C Peru), but hybridization not yet demonstrated. Monotypic.

Distribution. E slope of Andes in C Peru.



Descriptive notes. 10-11 cm; male 6-0 g, female 5-5 g. Male has straight, medium-sized bill, upper mandible blackish, lower reddish with dark tip; upperparts and flanks brilliant to bronze-green; centre of underparts whitish, spotted greenish on sides of chin and throat; undertail-coverts whitish, sometimes basally golden green; rectrices greyish-green to golden green without white basal portions. Differs from rather similar *L. chionogaster* by duller, more olive tone to green of upperparts. Female has chin and throat light cream-coloured, the latter more heavily spotted green. Immature has cream-coloured parts extending to belly.

Habitat. Forest edges, clearings and second growth in the humid subtropical zone between 1000 and 2500 m.

Food and Feeding. Nectar of various plant species, also small arthropods.

Breeding. Poorly known. Breeding has been observed in Jan, possibly representing the seasonal peak; additionally, nest-building was recorded in Jul. Nest cup-like, with moss, plant wool, lichen and cobweb; often placed on horizontal branches of smaller trees. Clutch size 2; incubation by female; no data exist on incubation and fledging periods.

Movements. Probably some local dispersal.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Peruvian East Andean Foothills EBA. Fairly common breeder in Pasco, and around Machu Picchu in Cuzco. In view of its limited distribution and the scant information available about its biology and ecological requirements, further field studies are needed to clarify the type of conservation measures required for this species.

Bibliography. Fjeldså & Krabbe (1990), Meyer de Schauensee (1982), Olrog (1968), Parker *et al.* (1982), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Taczanowski (1884), Terborgh *et al.* (1984), Zimmer (1950f).

139. Many-spotted Hummingbird

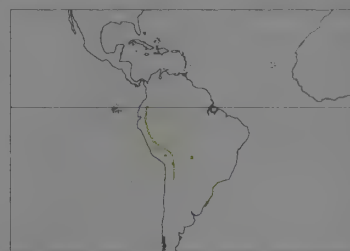
Leucippus hypostictus

French: Colibrí grivelé **German:** Tropfenkolibri **Spanish:** Colibrí Moteado

Taxonomy. *Aphantochroa hyposticta* Gould, 1862, Ecuador.

Sometimes placed in monospecific genus *Tuphrospilus*; alternatively, in past, sometimes placed with *L. taczanowskii* and *L. chloroceryx* in *Talaphorus*. Proposed race *peruvianus* fits well into overall pattern of variation within the species, so subspecific status cannot be maintained. Monotypic.

Distribution. E Andes in E Ecuador, E Peru and C & SE Bolivia to SW Brazil (W Mato Grosso) and NW Argentina.



Descriptive notes. 10.5-11.4 cm; 6-7-7.2 g. Male has slightly curved, medium-sized black bill; upperparts grass green to coppery bronze, white postocular spot; underparts white, heavily spotted green except on central belly; tail blue-green, tipped dusky grey. Female similar to male but lighter underneath. Immature like adult, but has buffy fringes to head feathers.

Habitat. Forest and forest edges along small ravines of Andean foothills at 400-1000 m. Most numerous around 600 m. Forages from low to mid-strata, usually inside vegetation.

Food and Feeding. Nectar of flowering shrubs, terrestrial bromeliads, vines, trees, including *Palicourea*, *Centropogon*, *Pitcairnia*, *Passiflora* and *Inga*. Insects are taken in the air by hawking, often in clearings or above small streams.

Breeding. Probably Jan-May; one active nest from Apr. Bulky cup-shaped nest of fine rootlets and moss is built low (c. 0-5 m) on tree trunk. Clutch size 2; incubation 14-15 days, by female; fledging at 20-22 days.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Common throughout range. A little-studied species which seems to tolerate secondary growth. Occurs between Tena and Coca (NE Ecuador), and between Cuzco and Manu (Peru).

Bibliography. Albuja & De Vries (1977), Best *et al.* (1997), Butler (1979), Fjeldså & Krabbe (1990), Forrester (1993), Grantsau (1988), Meyer de Schauensee (1982), Olrog (1968), Parker *et al.* (1982), Remsen & Traylor (1989), Ruschi (1982a, 1986), Stotz *et al.* (1996), Todd (1942), Zimmer (1950f).



Genus *AMAZILIA* Lesson, 1843

140. Rufous-tailed Hummingbird

Amazilia tzacatl

French: Ariane à ventre gris **German:** Braunschwanzamazilie **Spanish:** Amazilia Tzacatl
Other common names: Rieffer's Hummingbird; Escudo Hummingbird (*handleyi*)

Taxonomy. *Trochilus Tzacatl* De la Llave, 1833, Mexico.

Forms a superspecies with *A. castaneiventris*, but not, as sometimes suggested, with *A. rutila* and *A. yucatanensis*, given considerable distributional overlap with former in Central America. Race *handleyi* has been treated as a distinct species, due mainly to its much larger size, but this is untenable due to zone of morphometric intergradation with nominate in Bocas del Toro Archipelago. Validity of race *fuscaudata* has been questioned, but supported by morphometric characters. "*A. bangsi*" is a hybrid of present species and *A. rutila*. Four subspecies recognized.

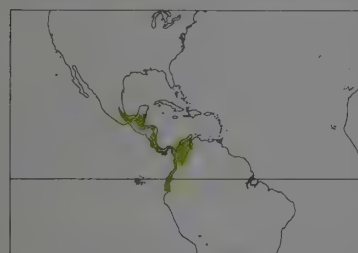
Subspecies and Distribution.

A. t. tzacatl (De la Llave, 1833) - CE (possibly NE) Mexico to C Panama.

A. t. handleyi Wetmore, 1963 - I Escudo de Veraguas (off NW Panama).

A. t. fuscaudata (Fraser, 1840) - N & W Colombia and W Venezuela.

A. t. jucunda (Heine, 1863) - SW Colombia and W Ecuador.



Descriptive notes. 8-11 cm; male 5.5 g, female 5.2 g, race *handleyi* (unsexed) 7.0 g. Male has bill straight, medium-sized, fleshy red with dark tip, or upper mandible blackish; upperparts, flanks and belly golden green to bronze-green; throat glittering golden green, sometimes with a turquoise gleam in certain lights; belly ashy grey to greyish-brown; tail rufous, rectrices with bronze-green to copperish margins. Female similar to male, but has greyish subterminal bars on throat feathers, and white belly. Immature darker greyish towards belly. Race *handleyi* considerably larger and heavier, slightly darker bronze-green above; *fuscaudata* is smaller in all

measurements; *jucunda* has longer bill in relation to size, and narrowed margins in outer rectrices.

Habitat. Edges of humid evergreen forest, clearings, plantations of bananas or coffee, human habitations; usually not inside dense forest. Often in second growth and semi-open, thicket-rich areas; in South America, partially in gallery forest and mangrove. Ranges in Costa Rica and Panama through the subtropical belt occasionally into lower montane zones, from sea-level up to 1200 m. On islands of Panama and in Colombia, inhabits primary forest as well as bushy coastal habitats, even beaches; in northern Andes, found up to 2500 m, occasionally higher. In SW Colombia, race *jucunda* ranges from lowlands into the subtropical zone with wet, open forest elements, up to 2500 m.

Food and Feeding. Nectar and arthropods. Found in all strata from near the ground to the more open sides of tree crowns; frequently gathers in some numbers with conspecifics or congeners such as *A. amazilia* and *A. rutila*. Generalist forager; feeding has been observed at a wide variety of plants, including *Antigonon*, *Callistemon*, *Clitoria*, *Costus*, *Iseria*, *Hamelia*, *Heliconia*, *Stachytarpheta*, *Tabebuia*, *Lantana*, and diverse cultivated tree species, especially banana and coffee; sometimes along roadsides. Occasionally perches at the end of the petals of larger flowers, or on adjacent blossoms. In Colombia, use of holes in corollae of *Thunbergia* flowers previously pierced by Bananquits (*Coereba flaveola*) observed. Gleans insects and small spiders from leaves and branches. Mainly territorial, also when associated in groups; intruders, even larger trochilids, Hesperidae butterflies, and euglossine bees are sometimes attacked in "diving" flight.

Breeding. Almost all year round. In northern parts of Central America, nesting records Dec-Sept; in Mexico, mainly Mar-Aug, correlated with moulting period Sept-Dec. In Costa Rica, breeding period peaks Jan-May, according to dry season; birds on Pacific slope breed May-Nov, on Caribbean slope Oct-Jun; in Panama and South America, Jan-Apr. Favourite nest-sites are horizontal branches in smaller trees or shrubs, mostly 2-5 m (<1.7 m) above ground; sometimes nest placed in fork. Nest material varies, and includes plant down, yellowish-brown to greyish-brown fibres, cobweb, pieces of dead leaves, and lichens in the form of a compact cup. Clutch size 2; incubation 15-16 days, by female; chick blackish, with buff down; fledging at 18-22 days. May form very loose "colonies", where stealing of nesting material has been observed. After loss of a nest, construction of a new one may start within one week.

Movements. In humid regions generally more sedentary than in arid areas; more or less all year round inhabitant of tropical wet forests. Northernmost population probably winters along Pacific and Caribbean coast of Mexico, i.e. Guerrero and Yucatán. Vagrants may occur farther north of the range limit and have been recorded from S Texas in summer and autumn. Migrational trends not known in other parts of Central America; race *handleyi* probably sedentary. Seasonal movements are known from Colombia and Ecuador since altitudinal distribution varies with flowering periods of food plants, though to what extent remains to be studied.

Status and Conservation. Not globally threatened. CITES II. Common to very common in most of range, e.g. Canal Zone of Panama. Less abundant in regions with tropical dry forest, dense rainforest and lower montane forest. Readily accepts man-made habitats, thus one of the most frequent trochilids in areas of habitation and cultivation. Race *handleyi*, with tiny range, may require monitoring.

Bibliography. Andrie (1967), Bangs (1930), Bent (1940), Berg (1994), Binford (1989), Blake & Loiselle (1991), Bloch *et al.* (1991), Borrero (1965, 1972, 1975), Boyden (1978), Brosset (1964), Brown & Bowers (1985), Butler (1932a, 1932b), Carriker (1910), Chapman (1917), Darlington (1931), Deignan (1936), Edwards & Tashian (1959), Eisenmann (1957), Fairchild *et al.* (1977), Feinsinger (1976, 1977, 1980), Fjeldså & Krabbe (1990), Friedmann *et al.* (1950), Fritsch & Schuchmann (1988), Gray (1958), Hartert (1898), Hartman & Lessler (1963), Heath (1932), Heine (1863), Hilty (1985, 1997), Hilty & Brown (1986), Howell, S.N.G. & Webb (1995a), Howell, T.R. (1957), Hughes (1970), Johnsgard (1997), Kennard & Peters (1928), Labude (1981), Land (1963a, 1970), Leck (1972), Lowery & Dalquest (1951), Mayr & Short (1970), Meyer de Schauensee (1949), Meyer de Schauensee & Phelps (1978), Monroe (1968), Munves (1975), Nicéforo (1940), Noedal (1981), Oberholser (1902), Olson (1997), Paynter (1955), Peters (1931), Poley (1968a), Pople *et al.* (1997), Primack & Howe (1975), Ralph & Chaplins (1973),

Richmond (1899), Ricklefs (1976), Ridgely & Gwynne (1989), Ridgway (1911), Russell (1964), Rutgers & Norris (1972), Schuchmann & Schmidt-Marloh (1979b), Schuchmann *et al.* (1979), Skutch (1931, 1945, 1949, 1950, 1951, 1952, 1958, 1964a, 1966, 1972, 1981), Slud (1960, 1964), Smithe & Paynter (1963), Snow & Snow (1980), Stiles (1975, 1978a, 1980, 1985c, 1995b), Stiles & Skutch (1989), Stone (1918), Stotz *et al.* (1996), Tashian (1952), Todd (1942), Wagner (1957b), Wetmore (1943, 1959, 1963, 1968a), Williams & Tobias (1994), Wolf *et al.* (1972), Zimmerman (1957a).

141. Chestnut-bellied Hummingbird

Amazilia castaneiventris

French: Ariane à ventre roux **German:** Braunbauchamazilie **Spanish:** Amazilia Ventricastaña

Taxonomy. *Amazilia castaneiventris* Gould, 1856, Santa Fé de Bogotá, Colombia.

Forms a superspecies with *A. tzacatl*, but not, as sometimes suggested, with *A. rutila* and *A. yucatanensis*. Monotypic.

Distribution. W slope of E Andes of NC Colombia.



Descriptive notes. 9 cm. Male has straight, medium-sized, blackish bill with fleshy red base to lower mandible; upperparts bronze-green; throat and upper breast glittering golden green; lower belly, undertail-coverts and rectrices chestnut-coloured, latter with greenish borders. Female similar to male, but with white subterminal bars on upper throat feathers, and slightly paler belly. Immature has rufous feather borders on neck and rump.

Habitat. Inhabits bushy canyons and edges of lower montane humid forest. Mainly found between 500 and 1500 m, rarely up to 2000 m; one lowland record at 120 m.

Food and Feeding. Forages for nectar at various plant species, including *Salvia* and *Trichanthera*; diet also includes small arthropods.

Breeding. Breeding condition of specimens suggests season from Aug to Dec. Clutch size 2; incubation by female; no data on incubation or fledging periods.

Movements. May occur at lower altitude after breeding season.

Status and Conservation. ENDANGERED. CITES II. Restricted-range species; present in Nechi Lowlands EBA and Colombian East Andes EBA. By far the rarest representative of the genus; current status and population size unknown, and species has not been observed during the past two decades; formerly locally common in Santander. Due to insufficient information on distribution and biology, especially habitat requirements, suitable protection measures have yet to be proposed or enforced; has presumably suffered from the extensive deforestation within its range.

Bibliography. Berlioz (1962), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Feinsinger, Tiebout, Young & Murray (1991), Hilty (1985), Hilty & Brown (1983, 1986), Linhart *et al.* (1987), Meyer de Schauensee (1982), Olrog (1968), Paynter & Taylor (1981), Renjifo *et al.* (1997), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Warren (1966), Wege & Long (1995).

142. Amazilia Hummingbird

Amazilia amazilia

French: Ariane de Lesson **German:** Rostbauchamazilie **Spanish:** Amazilia Costeña

Taxonomy. *Orthorhynchus* [sic] *Amazilia* Lesson, 1826, Callao de Lima, Peru.

Forms a superspecies with *A. alticola*, with which formerly considered conspecific; differs in coloration, song repertoire and habitat requirements, with no hybridization yet reported where the two are probably parapatric in S Ecuador. Race *leucophaea* frequently misspelt as *leucophaea*. Four subspecies recognized.

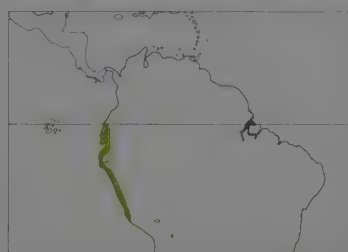
Subspecies and Distribution.

A. a. dumerilii (Lesson, 1832) - W of Andes from W Ecuador to N Peru; E slope in SE Ecuador (upper Zamora Valley).

A. a. leucophaea Reichenbach, 1854 - NW Peru.

A. a. amazilia (Lesson, 1826) - W Peru.

A. a. caeruleigularis Carriker, 1933 - SW Peru (Nazca Valley).



Descriptive notes. 9-11 cm; male 5.0 g, female 4.5 g. Male has straight, medium-sized, flesh red bill with dark tip; golden green upperparts; throat glittering golden to turquoise green, normally without white patch; lower breast and belly rufous; uppertail-coverts and tail rufous, rectrices laterally bronze-green. Female strongly resembles male, but sometimes has more conspicuous white subterminal bars on chin and throat feathers; lighter rufous on belly. Immature has brownish borders on feathers of upperparts. Races *dumerilii* and *leucophaea* smaller, with white chin feathers, throat patch and centre of belly, and *leucophaea*

is bronze-green above; birds of race *dumerilii* from W Ecuador show greyish-green rectrices; *caeruleigularis* distinguished by glittering violet-blue throat patch.

Habitat. In contrast to other members of genus, prefers semi-arid to arid open, partially coastal, habitats with scrub, thorn forest, xerophytic steppe and desert areas. Rarer in forested areas, mainly in the tropical zone along the Pacific coast. The races *dumerilii* and *leucophaea* reach sub-montane, sub-tropical zones. Also common in cultivation and habitations, even parks and gardens within cities such as Lima. Ranges mostly from sea-level to 1000 m (races *amazilia*, *dumerilii*). Race *leucophaea* shows greatest altitudinal tolerance of all subspecies, reaching montane elevations of up to 2700 m in Cajamarca;

On following pages: 143. Loja Hummingbird (*Amazilia alticola*); 144. Buff-bellied Hummingbird (*Amazilia yucatanensis*); 145. Cinnamon Hummingbird (*Amazilia rutila*); 146. Plain-bellied Emerald (*Agyrtia leucogaster*); 147. Versicolored Emerald (*Agyrtia versicolor*); 148. Blue-green Emerald (*Agyrtia rondoniae*); 149. White-chested Emerald (*Agyrtia brevirostris*); 150. Andean Emerald (*Agyrtia franciae*); 151. White-bellied Emerald (*Agyrtia candida*); 152. Azure-crowned Hummingbird (*Agyrtia cyanocephala*); 153. Violet-crowned Hummingbird (*Agyrtia violiceps*); 154. Green-fronted Hummingbird (*Agyrtia viridifrons*).

however, mainly restricted to sub-montane elevations at 500–1500 m. Race *caeruleigularis* apparently restricted to desert-like, sub-montane habitats between 600 and 700 m.

Food and Feeding. Feeds on nectar of flowering *Erythrina*, *Psittacanthus*. Catches small insects and spiders. Male establishes territory; interspecific competition with other trochilids like *Leucippus baeri* and *Myrmia micrura* has been observed.

Breeding. Breeds all year round. Nest cup-like, 3 cm high, made of plant wool, brown fibres, white seed pappi, fixed with cobweb. Nest-sites include tops of overhanging and flat branches, sometimes ends of horizontal branches, c. 1–2.5 m above ground. In Ecuador, nests were found in cypress and porotillo bushes; during rainy season often in scrub with dense foliage. Clutch size 2; incubation 16–18 days, by female; chick blackish, with buff down; fledging period 17–25 days.

Movements. Some altitudinal dispersal after main breeding season.

Status and Conservation. Not globally threatened. CITES II. Common to uncommon along the Pacific coast and some Andean valleys of the Pacific slope; the commonest trochilid regionally. Race *dumerilii*, mainly of W Andes, known on E Andean slope only from upper Zamora Valley (SE Ecuador), where probably isolated from western populations. Southernmost race *caeruleigularis* is extremely local and occurs only in the Nazca Valley; probably still common there. Although no special measures for its protection have been taken, this race may profit from the geohistorical importance of the area, which contains unique Inca cultural monuments.

Bibliography. Baron (1897), Becker & López (1997), Berg (1994), Berlioz (1932c), Best & Clarke (1991), Best *et al.* (1997), Butler (1979), Carriker (1933), Chapman (1926), Elgar (1986, 1987), Fjeldså & Krabbe (1990), Koepecke (1970), Landman (1991), Lanyon (1975), Marchant (1959, 1960), Mischler (1986), Parker, Parker & Plenge (1982), Parker, Schulenberg *et al.* (1995), Pople *et al.* (1997), Schulenberg & Parker (1981), Stotz *et al.* (1996), Williams & Tobias (1994), Zimmer (1930, 1950f).

143. Loja Hummingbird

Amazilia alticola

French: Ariane alticole

German: Lojaamazilie

Spanish: Amazilia de Loja

Taxonomy. *Amazilia alticola* Gould, 1860, Puna district, Peru; error = Loja, Ecuador.

Forms a superspecies with *A. amazilia*, of which formerly considered a race; differs in coloration, song repertoire and habitat requirements, and probably parapatric with *A. amazilia dumerilii* in Casanga Valley (C Loja), where no interbreeding yet observed. Monotypic.

Distribution. Andes of S Ecuador; doubtfully N Peru.



Descriptive notes. 10–11 cm; male 6–5 g, female 5–5 g. Male has straight, medium-sized bill, fleshy red with dark tip; upperparts golden green; underparts mainly whitish, with green spots on chin and upper throat; cinnamon-rufous more reduced on breast than in *A. amazilia*; nearly all rectrices rufous, except for the innermost which show greenish traces; colour of undertail-coverts varies from pure white to rufous. Female has more whitish on chin; mostly lacks rufous sides. Immature has brownish borders on neck, lower back and rump feathers.

Habitat. Inhabits edges of cloudforest, clearings, semi-open to open scrub, and bushy savanna of the sub-montane zone. Recorded between 1000 and 2200 m but commonest above 1500 m.

Food and Feeding. Poorly known. Forages for nectar at flower corollas of medium length, where occasionally territorial. Feeds on small arthropods in the air and gleans them from leaves.

Breeding. Nov–Mar. Nest is an open cup, saddled on horizontal branch to which it is fixed with cobweb; made of plant down and decorated on the outside with lichens. Clutch size 2; incubation by female; chick blackish, with some buff dorsal down; no data exist on duration of incubation or fledging.

Movements. Unknown in detail; probably sedentary. May occur at lower altitudes after reproduction. **Status and Conservation.** Not globally threatened. CITES II. Restricted-range species; present in Southern Central Andes EBA. Common to locally common in suitable habitats; however, probably threatened by habitat destruction, in particular deforestation. As a result of this, the preferred cloudforest habitats are becoming more and more isolated from each other, which explains the species' increasingly rather patchy distribution.

Bibliography. Best *et al.* (1997), Bloch *et al.* (1991), Chapman (1926), Hüning (1999), Williams & Tobias (1994), Zimmer (1950f).

144. Buff-bellied Hummingbird

Amazilia yucatanensis

French: Ariane du Yucatan

German: Fahlbauchamazilie

Spanish: Amazilia Yucateca

Other common names: Fawn-breasted/Yucatan Hummingbird

Taxonomy. *Trochilus yucatanensis* Cabot, 1845, Yucatán, Mexico.

Forms a superspecies with *A. rutila*, but not, as sometimes suggested, with *A. tzacatl* and *A. alticola*. Race *cerviniventris* formerly treated as a distinct species, including race *chalconota*. Three subspecies recognized.

Subspecies and Distribution.

A. y. chalconota Oberholser, 1898 - extreme S USA (Texas) to NE Mexico (S to San Luis Potosí).

A. y. cerviniventris (Gould, 1856) - E Mexico (Veracruz, Puebla, Chiapas).

A. y. yucatanensis (Cabot, 1845) - SE Mexico (Tabasco, Campeche, Yucatán), N Belize and NW Guatemala; erroneously reported from Honduras.

Descriptive notes. 10–11 cm; male 4–5 g, female 4–0 g. Male has straight, medium-sized bill, fleshy red with dark tip; upperparts golden to bronze-green; throat glittering golden green; belly and undertail-coverts chestnut; tail slightly forked; central rectrices and upperpart-coverts greenish, or chestnut as outer rectrices, with bronze margins, narrowed towards tips. Female has dark upper mandible, whitish subterminal bars on throat feathers, and paler belly and undertail-coverts. Immature has duller crown, brownish borders on neck and rump feathers and less forked tail. Coloration of belly reflects intergradation between races, darkest in nominate race, becoming successively paler in *cerviniventris* and *chalconota*; *chalconota* has silky gloss on throat; *cerviniventris* has shorter wings and tail.

Habitat. Race *chalconota* prefers rather open habitats, like pine-oak forests, semi-arid coastal shrub, second growth, sometimes along ravines or smaller streams; in Texas, also inhabits patches



Breeding. On Yucatán Peninsula, Jan–Apr; in NE part of range, regularly Feb–Jul, with peak Mar–Jun; in Texas, mid Apr–mid Aug. Nest cup-shaped, small or relatively large and heavy, saddled on small branch or fork of twig, 1–3 m above ground; consists of vegetation fibres, pieces of herb stem, plant down, often of *Gossypium*; covered with lichens, dried blossoms, plant fibres, or pieces of bark, fixed with spiders' webs. Nest-sites are usually located in smaller trees and bushes like willow, hackberry, *Cordia*, or *Pithecellobium*; sometimes built beside a forest path or road. Clutch size 2; incubation by female; no data exist on incubation and fledging periods; chick buff with black dorsal down.

Movements. Partially migratory. Generally in lower numbers in breeding range Oct–Apr. Individuals of race *chalconota* migrate irregularly in autumn or winter NE along Gulf of Mexico coast, reaching Louisiana, Mississippi and Florida; rarely even farther north; southward-directed migration recorded in Mexico as far as Veracruz. Race *cerviniventris* has been recorded in late summer from SW Campeche (Yucatán Peninsula). Nominate birds are presumed to winter further south within Mexico in Tabasco and Chiapas. Not reported in winter on the Pacific slope.

Status and Conservation. Not globally threatened. CITES II. Usually, an abundant to common breeder, at least locally. Race *chalconota* has become a rare breeder in Rio Grande delta, due to rapid destruction of breeding habitat by spread of agriculture and pastures, use of biocides, and road construction. Race *yucatanensis* becomes uncommon to rare along its southern limits in Petén, Guatemala. Status for Honduras, either as migrant or breeding species, is questionable; in view of specimens supposedly of present species that were subsequently identified as hybrids of *A. tzacatl* x *A. rutila*, possible sightings require conclusive confirmation, particularly if no clear indication of regular occurrence is given.

Bibliography. Andrie (1967), Baicich & Harrison (1997), Bendire (1896), Bent (1940), Binford (1989), Bjelland & Ray (1977), Brewer (1878), Chávez-Ramírez & Moreno (1999), Davis (1952), DeGraaf & Rappole (1995), Ford (1938), Friedmann *et al.* (1950), Gehlbach *et al.* (1976), Griscom & Crosby (1926), Hamilton (1978), Howell & Webb (1995a), Johnsgard (1997), Kale (1985), Kaufman (1996), Land (1970), Lowery (1974), Lowery & Dalquest (1951), Luckner (1992), Lynch (1992), Martins *et al.* (1954), Mayr & Short (1970), Merrill (1877), Monroe (1968), Muth (1988), Newfield (1984), Oberholser (1974), Ogden (1990), Paynter (1955), Pickens (1935b), Purrington (1981, 1988), Ridgway (1911), Russell (1964), Sargent & Sargent (1996b), Stevenson (1953), Stotz *et al.* (1996), Sutton & Burleigh (1940), Sutton & Pettingill (1942), Todd (1942), Waide & Hailman (1977), Warner & Mengel (1951), Wauer (1998), Zimmerman (1957a).

145. Cinnamon Hummingbird

Amazilia rutila

French: Ariane cannelle

German: Zimtbauchamazilie

Spanish: Amazilia Canela

Taxonomy. *Ornismya rutila* DeLatre, 1843, Acapulco, Guerrero, Mexico.

Forms a superspecies with *A. yucatanensis*, but not, as sometimes suggested, with *A. tzacatl* and *A. alticola*, given extensive sympatry with former. Formerly listed as *A. cinnamomea*, but this name was unavailable. Race *graysoni* has sometimes been considered a separate species. Validity of race *diluta* has been doubted because of intergradation towards nominate birds. Name *saturata* is synonym of *corallirostris*. "*A. bangsi*", known from a single Costa Rican specimen, is hybrid of present species and *A. tzacatl*. Populations from Yucatán, Honduras, Nicaragua and Costa Rica, formerly attributed to nominate, are more appropriately placed in *corallirostris* on basis of morphology and biogeography. Four subspecies recognized.

Subspecies and Distribution.

A. r. diluta van Rossem, 1938 - NW Mexico (Sinaloa, Nayarit).

A. r. graysoni Lawrence, 1867 - Is Tres Marias (off W Mexico).

A. r. rutila (Lesson, 1842) - W & SW Mexico (Jalisco to Oaxaca).

A. r. corallirostris (Bourcier & Mulsant, 1846) - S & SE Mexico (from Chiapas and Yucatán) to Costa Rica.



Descriptive notes. 10 cm; male 5–0 g, female 4–5 g. Male has straight, medium-sized bill, fleshy red with dark tip; upperparts golden to bronze or copper-green above; underparts entirely rufous, chin feathers fringed greyish; tail and parts of upperpart-coverts rufous, tips of rectrices bronze-green to purplish. Female has blackish upper mandible, darker chin, and less rufous below. Immature has feathers of upperparts bordered with rufous. Race *diluta* has paler underparts; *graysoni* is considerably larger in all morphometric characters, bill slightly decurved; *corallirostris* has darker underparts, with chin more conspicuously spotted

white, bill in some individuals more coral red.

Habitat. Deciduous and semi-deciduous forests, thorn forests, forest edges, bushy savannas, second growth and around human habitation; mainly in the arid tropical zone. May occur in dense forest but avoids closed gallery forest. On islands such as offshore cays of Belize, found in low coastal scrub vegetation and coconut groves. Ranges from sea-level to 1700 m.

Food and Feeding. Nectar and insects. Often gathers around flowering trees or bushes, sometimes with congeners like *A. tzacatl*. Feeds on *Genipa*, *Luehea*, *Tabebuia* and other trees, shrubs like *Helicteres*, various herbs such as *Lamorouxia*, and vines such as *Combretum*. Perches relatively low down, but shows less feeding height preferences than other associated trochilid species; thus found both in lower and taller trees, usually feeding 6–15 m from ground; otherwise, less than 5 m in lower vegetation. Male defends territory that is normally established on the exterior of a tree crown, and defended against other hummingbirds like *Saucerottia saucerrottei* or *Campylopterus curvieri*, large bees, but rarely against passerines. Insects are caught in the air by hawking.

Breeding. Almost all year round. In W Mexico, nesting or birds in breeding condition were observed May-Feb; in E Mexico (Yucatán), birds in breeding condition were registered Mar-Apr; in El Salvador, Jul-Oct; in Costa Rica, nesting lasts from Dec to Jun, varying with the start of the dry season. Race *graysoni* seems to have prolonged nesting season, with breeding records from nearly all months except Sept and Dec, due to less restricted flower abundance than in mainland habitats. Nest cup-shaped, of plant down, treefern scales, and cobweb; 1-5 m above ground in shrubs or understorey at forest edges. Clutch size 2; incubation by female. No further information.

Movements. Sedentary in Is Tres Marias, partially migratory on mainland, especially N populations. Wintering birds in W Mexico were recorded from Sinaloa and Durango, in E Mexico from N part of Yucatán Peninsula.

Status and Conservation. Not globally threatened. CITES II. Common to very common in most parts of range, but mainly restricted to lower tropical zones with arid vegetation types. In Costa Rica, occurs in several protected areas, e.g. Santa Rosa, Palo Verde and Barra Honda National Parks. Race *graysoni* is confined to Is Tres Marias, where it is a common resident.

Bibliography. Arizmendi & Ornelas (1990), Bailey (1906), Bangs (1930), Binford (1989), Carriger & Meyer de Schauensee (1935), Calvo & Blake (1998), DeBenedictis (1994), Des Granges (1979), Des Granges & Grant (1980), Erickson (1977), Friedmann *et al.* (1950), Gass & Montgomerie (1981), Grant, P.R. (1966), Grant, P.R. & Cowan (1964), Howell & Webb (1995a), Howell & Johnston (1993), Hutto (1985), Johnson (1997), Land (1962, 1970), Lynch (1992), Mayr & Short (1970), Meadows (1979), Monroe (1968), Montgomerie (1979, 1984), Newfield (1996), Paynter (1955), Ridgway (1911), Rowley (1966, 1984), Russell (1964), Schemske (1975a, 1975b), Slud (1964, 1980), Stager (1957), Steinbacher (1958), Stiles & Wolf (1970), Stiles & Skutch (1989), Stiles & Wolf (1970), Stotz *et al.* (1996), Tashian (1953), Tramer (1974), Urdvary (1983), Wagner (1946a), Wolf (1970).

Genus AGYRTRIA Reichenbach, 1854

146. Plain-bellied Emerald

Agyrtia leucogaster

French: Ariane vert-doré **German:** Hellbauchamazilie **Spanish:** Amazilia Ventrianca

Taxonomy. *Trochilus leucogaster* J. F. Gmelin, 1788, Cayenne.

Genus usually merged into *Amazilia*. Race *bahiae* initially described based erroneously on characters of nominate birds; its validity has thus been questioned by later taxonomists. Two subspecies recognized.

Subspecies and Distribution.

A. l. leucogaster (J. F. Gmelin, 1788) - E Venezuela, the Guianas and NE Brazil.

A. l. bahiae Hartert, 1899 - E Brazil from Pernambuco to Bahia.



Descriptive notes. 9-10 cm; male 4-5 g, female 4-3 g. Male has bill straight to slightly decurved, blackish except for fleshy red base of lower mandible; crown and sides of neck glittering golden green, rarely with turquoise reflections; rest of upperparts, flanks and sides of throat golden to bronze-green; centre of throat, underparts and undertail-coverts white; inner rectrices bronze-green to bronze, outer rectrices bluish-black; tail slightly forked. Female very similar to male, but has more greenish spots on sides of throat and greyish-green tail tips. Immature has brownish feather margins on back. Race *bahiae* has longer bill and

wings; generally less bronze in coloration.

Habitat. Mangroves, especially *Avicennia*, forest edges, second growth, *cerrado*, *caatinga*, plantations, parks and gardens. Occurs mainly close to sea-level; in Venezuela occasionally up to 250 m.

Food and Feeding. Forages for nectar at herbs and low down at trees and shrubs; preferred plant families are Leguminosae, Vochysiaceae, Musaceae, Acanthaceae, Heliconiaceae, Bignoniaceae, Malvaceae, Bromeliaceae, Anacardiaceae, Verbenaceae and Passifloraceae. Catches small insects in flight by hawking.

Breeding. Recorded Jul-Aug in the Guianas and NE Brazil. Nest cup-shaped, made of plant wool, and sometimes Bromeliaceae, and leaves and other parts of Bombaceae; outer walls decorated with lichen; placed on horizontal branch or in fork of smaller tree or bush, usually less than 5 m above ground, in mangroves sometimes close to water surface. Clutch size 2; incubation 14 days, by female; fledging at 20-25 days.

Movements. Some local dispersal.

Status and Conservation. Not globally threatened. CITES II. A rather common resident of the coastal Guianas and Brazil, especially in mangrove forests. Status in the Brazilian parts of the range needs further clarification since the range boundaries remain unclear, in particular the limits of distribution of the two races. Records of the species away from the Atlantic coast are rare, for instance at Cerro El Trueno, Bolívar (S Venezuela).

Bibliography. Avelledo (1955), Bangs & Penard (1918), Berlepsch (1908), Chubb (1916), Forrester (1993), Grantsau (1988), Hartert (1899a), Haverschmidt (1955a), Haverschmidt & Mees (1994), Jouanin (1948), Meyer de Schauensee & Phelps (1978), Ruschi (1949a, 1981-1982, 1986), Sánchez (1995), Sargeant (1996), Sick (1993, 1997), Sneathlidge (1928a, 1928b), Snyder (1966), Stotz *et al.* (1996), Tobias *et al.* (1993), Tostain (1980), Tostain *et al.* (1992).

147. Versicolored Emerald

Agyrtia versicolor

French: Ariane versicolore **German:** Glanzamazilie **Spanish:** Amazilia Versicolor
Other common names: Cuyuni Emerald (*hollandi*)

Taxonomy. *Trochilus versicolor* Vieillot, 1818, Brazil.

Genus usually merged into *Amazilia*. Often considered to include *A. rondoniae* as a race, but probably better considered a distinct species, on basis of reported sympatry without interbreeding. Taxonomic confusion has been caused by occurrence of polymorphism within southern parts of range: birds from SE Brazil sometimes divided into two distinct races or even species, a green-throated inland one and a white-throated coastal one, but differences attributable to clinal variation within nominate race, and intermediates exist; coastal birds were listed as *brevirostris*, but this name now

considered to refer to the species formerly known as *A. chionopectus*. Distinctive race *hollandi* sometimes considered a separate species, and *millerii* and *nitidifrons* have also been suggested as constituting two further species. Validity of race *kubicheki* has often been questioned, but it appears justified on basis of morphology and biogeography. Race *viridiceps* of *A. franciae* sometimes placed in present species. Five subspecies recognized.

Subspecies and Distribution.

A. v. millerii (Bourcier, 1847) - tropical Colombia E of Andes, C Venezuela and Amazonian E Peru and N Brazil.

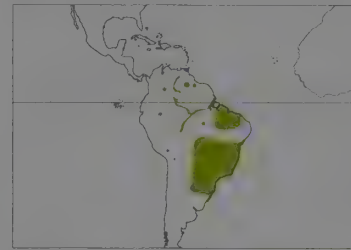
A. v. hollandi Todd, 1913 - SE Venezuela; possibly also W Guyana, where status unclear.

A. v. nitidifrons (Gould, 1860) - NE Brazil.

A. v. versicolor (Vieillot, 1818) - SE Brazil.

A. v. kubicheki (Ruschi, 1959) - NE Bolivia, E Paraguay, extreme NE Argentina and SW Brazil.

Precise limits of distribution very poorly known in Amazonia and NE Brazil.



Descriptive notes. 8-10 cm; male 4-0 g, female 3-5 g. Male has bill straight, medium-sized, upper mandible blackish, lower reddish except for dark tip; crown and cheeks dull bronze-green; upperparts shining golden green to bronze-green; chin and throat variable, pure white in coastal subpopulation, more spotted glittering green to entirely green in western subpopulation; centre of underparts white; sides of chest, flanks and undertail-coverts bronze-green, the latter fringed white; tail bronze-green, dark subterminal band on outer rectrices. Female has grey feather tips on outer rectrices. Immature has rufous borders to

crown, lower back and rump feathers; belly brownish. Race *millerii* has shorter bill, crown glittering turquoise, centre of throat entirely white; *hollandi* has bluish crown and cheeks and white throat; *nitidifrons* has turquoise to golden green glittering crown, cheeks and throat spots; *kubicheki* has significantly shorter bill, throat entirely glittering emerald green with turquoise reflections; females of races *kubicheki* and *nitidifrons* show conspicuous white subterminal bars on chin feathers.

Habitat. In northern parts of range, chiefly found at edges of cloud and rainforest and in gallery forest; ranges altitudinally from 50 m in the Amazon basin to 1250 m in the lower sub-montane zone of the eastern slope of E Andes; rarely above 1000 m in the Pantepui region of NE South America, with upper limit at 1700 m. In E and S Brazil, prefers more open habitats with scrub, *caatinga*, or *campo cerrado*; also found in suburban areas such as parks and gardens; mostly below 900 m.

Food and Feeding. Nectar and arthropods; feeds and perches at all levels. Has been observed to visit a great variety of plant families; prefers flowers with short or no corolla tubes, in particular Loganiaceae (*Buddleja*), Asteraceae (*Piptocarpha*), Bromeliaceae (*Tillandsia*, *Vriesea*), Amaryllidaceae (*Alstroemeria*), Zingiberaceae (*Inga*); also many species of Ranunculaceae, Passifloraceae, Bombaceae, Vochysiaceae, Verbenaceae, Labiataceae and Cactaceae. In orchards or suburban areas, common at flowering bushes or trees of *Heliconia*, *Eucalyptus* or *Citrus*. Small arthropods are taken from leaves or caught in the air by hawking.

Breeding. Almost all year round; in E Brazil, Oct-Mar. Nest cup-shaped, built of plant down and seeds of, among others, *Asclepias*, *Chorisia*, Bromeliaceae, *Typha*, or Graminae that are attached with cobweb; outer walls decorated with pieces of grey-red lichens; placed on a horizontal branch, usually 1-6 m above ground, occasionally up to 10 m. Clutch size 2; incubation 14 days, by female; fledging at 20-26 days, occasionally up to 32 days.

Movements. Generally sedentary, with some local movements.

Status and Conservation. Not globally threatened. CITES II. The southern races *versicolor* and *kubicheki* are more common and widespread than the northern representatives, except *millerii*. In Venezuela, *millerii* occurs almost exclusively south and east of the Orinoco, with only one record to the north in lower Orinoco basin (Monagas). Generally, distribution poorly understood as nearly all races show either unclear range limits or highly scattered distribution; as an example of the latter, race *hollandi* may be confined to a few valleys and tepuis of the SE Venezuelan highlands.

Bibliography. Abe *et al.* (1992), Bangs & Penard (1918), Barrowclough *et al.* (1997), Bech *et al.* (1997), Belton (1984), Berlioz (1934, 1964), Bond & Meyer de Schauensee (1943), Brooks *et al.* (1993), Burton (1971), Canevari *et al.* (1991), Cintra & Yamashita (1990), Friedmann (1948), Grantsau (1988), Griscom & Greenway (1941), Guix *et al.* (1992), Hartert (1899a), Hayes (1995), Hellmayr (1906, 1929), Hilty & Brown (1986), Lowen, Bartrina, Clay & Tobias (1996), Navas & Bo (1993), Nicéforo & Olivares (1967), Meise (1938), Meyer de Schauensee & Phelps (1978), Naumburg (1930), Oniki (1996), de la Peña (1994), do Rosário (1996), Ruschi (1959, 1967a, 1973d, 1981-1982, 1986), Saibene *et al.* (1996), Sánchez (1995), Sick (1993, 1997), Snow & Snow (1986), Stotz *et al.* (1996), Teixeira *et al.* (1987), Todd (1942), Viellard (1983, 1994), Willard *et al.* (1991), Willis (1992), Zimmer (1950f).

148. Blue-green Emerald

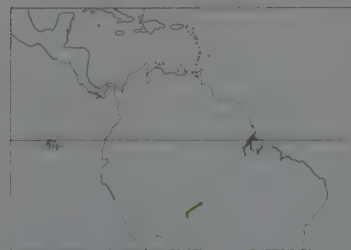
Agyrtia rondoniae

French: Ariane du Rondonia **German:** Blaugrünamazilie **Spanish:** Amazilia de Rondonia

Taxonomy. *Amazilia rondoniae* Ruschi, 1982, Porto Velho, Rondônia, Brazil.

Genus usually merged into *Amazilia*. Usually considered a race of *A. versicolor*, but on basis of reported sympatry without interbreeding, probably better considered a distinct species. Monotypic.

Distribution. Known only from right bank of R Madeira in WC Brazil (Rondônia) and N Bolivia.



Descriptive notes. 8.5-9.5 cm. Male has straight, short bill, upper mandible blackish, lower fleshy red with dark tip; crown, cheeks and chin azure blue; upperparts and flanks shining bronze-green; centre of underparts white; tail bronze-green with dark subterminal bars on outer rectrices. Female has more extensive turquoise green on neck sides; chin spotted bluish-green, due to broader white subterminal bars. Immature plumage unknown.

Habitat. Forests, *cerrado*, park-type landscapes along R Madeira at altitude of c. 100 m.

Food and Feeding. Forages for nectar at various trees and bushes like *Inga*; diet also includes tiny insects.

Breeding. No information available.
Movements. no information.

Status and Conservation. Not globally threatened. CITES II. Current status and distribution needs to be studied as population size and extent of range are unclear. Ecological requirements insufficiently known; perhaps threatened by deforestation, a situation that applies in particular to the Brazilian population.

Bibliography. Bahr (1995), Forrester (1993), Grantsau (1988), Hartert (1899a), Ruschi (1981-1982, 1982b, 1986), Sick (1993), Viellard (1994).

149. White-chested Emerald

Agyrtia brevirostris

French: Ariane à poitrine blanche

Spanish: Amazilia Pechiblanca

German: Kurzschnebelamazilie

Other common names: White-breasted Emerald

Taxonomy. *Ornismya brevirostris* Lesson, 1829, Guyana.

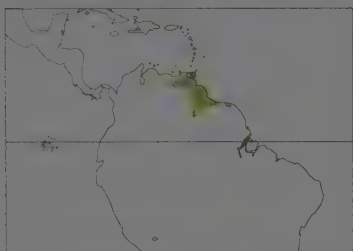
Genus usually merged into *Amazilia*. Species has normally been listed as *A. chionopectus*, as name *brevirostris* was believed to refer to *A. versicolor* with an erroneous type locality. With rectification of name and consequent revised type locality, race formerly listed as *whitelyi* becomes nominate, with name *whitelyi* as a synonym. Three subspecies recognized.

Subspecies and Distribution.

A. b. chionopectus (Gould, 1859) - Trinidad.

A. b. brevirostris (Lesson, 1829) - E Venezuela, Guyana, Surinam and extreme NC Brazil.

A. b. orienticola (Todd, 1942) - coastal French Guiana.



Descriptive notes. 9-10 cm; male 4-6 g, female 4-4 g. Male has straight, short, almost blackish bill; crown and cheeks iridescent turquoise green; upperparts shining bronze-green, becoming more copperish towards rump and tail; central underparts white; flanks and sides of chest bronze-green; undertail-coverts with golden green centres and white fringes; lateral tail feathers bronze to copperish, duller on upperside, with blackish subterminal bars below. Female has greyish tips on outer rectrices. Immature similar to female, but with yellowish to reddish base of lower mandible. Race *chionopectus* significantly larger in all

morphometric characters; *orienticola* has upperparts and flanks darker, more markedly bronze-coloured.

Habitat. Inhabits rainforest, semi-deciduous forest, and gallery forest, second growth, scrub, savanna and semi-cultivated land. On Trinidad, prefers more open valleys with plantations. Ranges from sea-level to 500 m; race *orienticola* apparently restricted to coastal habitats.

Food and Feeding. Forages for nectar at larger trees, including *Erythrina* and *Samanea*, smaller trees like *Calliandra*, herbs such as *Pachystachys*, and various species of Malvaceae, Leguminosae, Lorantaceae, Bignoniaceae, Vochysiaceae and Verbenaceae. Hunts for small insects in vegetation, or in the air by hawking.

Breeding. At least Dec-Apr. Nest cup-shaped, made of greyish plant fibres, decorated with lichen; placed on horizontal branch 1-7 m above ground. Clutch size 2; incubation by female; fledging period about 20 days.

Movements. No information available; most populations probably sedentary.

Status and Conservation. Not globally threatened. CITES II. Generally a common resident in semi-open, coastal areas. One of the commonest trochilids on Trinidad; adapts readily to man-made habitats. However, the status of some important mainland populations has not been studied recently, so there is no information on current abundance or potential threats. For example, race *orienticola* is considered to be very rare since only two specimens exist and there have been very few sightings; the most recent possible record was in 1987.

Bibliography. Bangs & Penard (1918), Belcher & Smoother (1936), Berlepsch (1908), Broom (1976), Chubb (1916), Deignan (1961), French (1991), Forrester (1993), Friedmann & Smith (1955), Grantsau (1988), Hartert (1899a), Haverschmidt (1955a), Haverschmidt & Mees (1994), Herklots (1961), Junge & Mees (1961), Meyer de Schauensee & Phelps (1978), Ruschi (1981-1982, 1986), Sargeant (1994a), Shingler (1969), Sick (1993, 1997), Snow & Snow (1972), Snyder (1966), Stotz *et al.* (1996), Tostain *et al.* (1992), Zimmer & Hilty (1997).

150. Andean Emerald

Agyrtia franciae

French: Ariane de Francia

German: Andenamazilie

Spanish: Amazilia Andina

Taxonomy. *Trochilus Franciae* Bourcier and Mulsant, 1846, Bogotá, Colombia.

Genus usually merged into *Amazilia*. Due to different crown colour, race *viridiceps* sometimes regarded as a separate species or treated as race of *A. versicolor*. "*A. veneta*" may be melanistic female of present species. Three subspecies recognized.

Subspecies and Distribution.

A. f. franciae (Bourcier & Mulsant, 1846) - NW & C Colombia.

A. f. viridiceps (Gould, 1860) - SW Colombia and W Ecuador.

A. f. cyanocollis (Gould, 1854) - Andes of N Peru.



Descriptive notes. 9-11 cm; male 5-6 g, female 5-3 g. Male has medium-sized, straight to slightly decurved bill, upper mandible blackish, lower coral red with dark tip; crown glittering violet-blue; cheeks and neck glittering golden to emerald green; rest of upperparts and flanks light to golden green, with more copperish tinge towards uppertail-coverts; centre of underparts white; tail bronze-green to copperish, sometimes with purplish tinge to inner rectrices. Female has crown less glittering, more turquoise blue to greenish. Immature male resembles female in crown coloration, also has brownish feather borders on entire upperparts; greyish

brown on flanks. Race *viridiceps* has green crown and significantly shorter tail; in race *cyanocollis*, crown patch extends to nape.

Habitat. Inhabits wet forest edges, second growth and clearings; in W Peru, also found in more arid, shrubby areas. Ranges in altitude from 600 to 2100 m; commonest above 1000 m, rarely in lowlands.

Food and Feeding. Forages for nectar at various heights, chiefly in middle to upper strata; may form feeding assemblies. Found at flowering herbs such as banana (*Musa*) or *Canna*, climbers like *Psammisia*, shrubs (*Hamelia*, *Cavendishia*), and trees, especially *Eugenia*. Trap-liner; often subordinate to territorial hummingbird species such as *Amazilia tzacatl* and *Saucerottia cyanifrons*. Occasionally hawks for insects in short sallies, close to or within vegetation.

Breeding. Almost all year round; birds in breeding condition have been recorded in Apr, May, Oct, Dec. Nest cup-shaped, fixed with cobweb, covered on outside with lichen. Clutch size 2; incubation by female; chick flesh-coloured, with buff down; no data exist on incubation and fledging periods.

Movements. Seasonal changes in altitude indicated by absence from breeding areas such as Anchicayá (SW Colombia), and by a few lowland records (e.g. in Colombia, at R Zapato).

Status and Conservation. Not globally threatened. CITES II. Fairly common to uncommon, but status of local populations poorly known. Abundance in certain places may vary with flowering season of plants. Present in La Planada Reserve, Nariño (S Colombia).

Bibliography. Becker & López (1997), Berlioz (1937), Best *et al.* (1997), Butler (1979), Chapman (1917, 1926), Davies *et al.* (1994), Grummi (1975), Hartert (1899a), Hilty (1977, 1997), Hilty & Brown (1986), Kirwan & Marlow (1996), Meise (1938), Meyer de Schauensee (1949, 1964, 1982), Miller (1963), Mobbs (1972c), Parker *et al.* (1982), Rutgers & Norris (1972), Salaman & Mazariegos (1998b), Snow & Snow (1980), Stotz *et al.* (1996), Warren (1966), Williams & Tobias (1994), Zimmer (1950f).

151. White-bellied Emerald

Agyrtia candida

French: Ariane candide

German: Bronzekopfamazilie

Spanish: Amazilia Cándida

Taxonomy. *Trochilus candidus* Bourcier and Mulsant, 1846, Cobán, Guatemala.

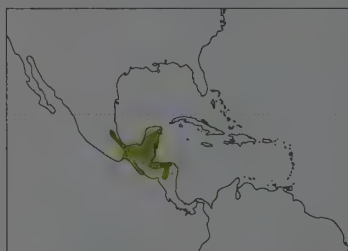
Genus usually merged into *Amazilia*. Race *genini* has been questioned on the basis of some intergradation with nominate in E Mexico. Three subspecies recognized.

Subspecies and Distribution.

A. c. genini Meise, 1938 - E to S Mexico.

A. c. pacifica Griscom, 1929 - SE Mexico (S Chiapas) and S Guatemala.

A. c. candida (Bourcier & Mulsant, 1846) - SE Mexico (Yucatán Peninsula) and Belize through N Guatemala and Honduras to Nicaragua.



Descriptive notes. 9-11 cm; male 3-8 g, female 3-4 g. Male has straight, short bill, blackish except for pinkish basal part of lower mandible; crown dark bronze-green; upperparts shining golden to bronze-green; throat, centre of underparts, and undertail-coverts white; tail bronze-green, dark subterminal band on outer rectrices. Female differs from male in spotted sides of throat and greyish tips to tail feathers. Immature has grey-brownish belly. Race *genini* has significantly longer, slightly broader bill; *pacifica* has longer, broader bill and longer wings.

Habitat. More confined to forests than most other congeners. Inhabits rainforest and cloudforest, wooded riverbanks, clearings, coffee and banana plantations. Nominates race and *genini* occur from sea-level to 1500 m, but mostly in the lower sub-montane zone below 1000 m; race *pacifica* found between 400 and 1000 m.

Food and Feeding. Diet includes nectar and small insects. Found in all strata; in forest interiors at tree tops, at lower levels outside forests. Food plants include trees like *Inga micheliana*, *Miconia trinervia* and *Trichospermum*, shrubs such as *Cephaelis* or *Hamelia*, and herbs (*Heliconia*); seasonal trap-lining recorded. Sometimes seen in groups with congeners, or together with other species; partially subordinate to *Amazilia tzacatl* among other species.

Breeding. In Mexico, laying has been reported Apr-May. However, breeding probably starts in Feb when singing activity occurs; birds in breeding condition have been observed until Sept. Nest cup-shaped, made of soft plant down and fibres; placed on a horizontal branch. One nest was found 2 m up in a *Guettarda* tree. Clutch size 2; incubation by female; no data exist on duration of incubation or fledging.

Movements. Wintering birds of the northern populations have been recorded from the Pacific slope of Oaxaca and Chiapas (Mexico). Wintering habitats include swamps and semi-deciduous forests. Strong seasonal movements are found in Oaxaca, where breeders occur in large numbers in lowland tropical evergreen forests from mid-Feb to Jul in the Atlantic region, where less common from mid-Jul to Nov, and absent in winter. Race *candida* accidental to Costa Rica; any have bred there in past, but no recent records.

Status and Conservation. Not globally threatened. CITES II. Common in the tropical lowlands along the Caribbean slope. Uncommon to rare at higher elevations and on the Pacific slope. Race *pacifica* restricted to scattered lowland and sub-montane rainforests in SE Mexico and S Guatemala; has suffered from extensive deforestation. Establishment of forest reserves appears necessary to protect remnant populations. Current status in Costa Rica unclear; a few older specimen records may indicate occurrence, at least formerly, as rare breeding species.

Bibliography. Andrie (1967), Atwood *et al.* (1991), Binford (1989), Bjelland & Ray (1977), Blake (1950a), Davis (1972), Dearborn (1907), Edwards & Tashian (1959), Feinsinger (1976), Friedmann *et al.* (1950), Griscom (1934), Hartert (1899a), Howell & Webb (1992a, 1995a), Johnson (1997), Land (1963a, 1963b, 1970), Lowery & Dalquest (1951), Lynch (1992), Meise (1938), Monroe (1968), Noctedal (1981), Paynter (1957), Phillips (1964), Ridgway (1911), Russell (1964), Rutgers & Norris (1972), Slud (1964), Smith & Paynter (1963), Stiles & Skutch (1989), Stotz *et al.* (1996), Sutton & Burleigh (1940), Tashian (1953), Wagner (1957b).

152. Azure-crowned Hummingbird

Agyrtia cyanocephala

French: Ariane à couronne azur

German: Blaukopfamazilie

Spanish: Amazilia Coroniazul

Other common names: Red-billed Azurecrown; Mosquitia Hummingbird (*chlorostephana*)

Taxonomy. *Ornismya cyanocephalus* Lesson, 1829, Brazil; error = Veracruz, Mexico.

Genus usually merged into *Amazilia*. Race *chlorostephana* has been suggested as possibly approaching species status, but nominate (in E of range) shows clinal variation in crown colour to-

wards *chlorostephana*. Birds from Belize S to N Nicaragua formerly separated as race *guatemalensis*, but specimens from C & E Guatemala, including type locality of *guatemalensis*, Dueñas, show strong intergradation with nominate birds from Chiapas (S Mexico). Proposed species "A. *microrhyncha*" (Honduras, Nicaragua), known from two specimens and separated in part on basis of unusually short bill, does not merit even subspecific recognition because characters appear to be based on individual variation or juvenile, probably of nominate. Two subspecies recognized.

Subspecies and Distribution.

A. c. cyanocephala (Lesson, 1829) - E & S Mexico to E Honduras and NC Nicaragua.

A. c. chlorostephana (Howell, 1965) - Mosquito Coast of E Honduras and NE Nicaragua.



Descriptive notes. 10-11 cm; male 5-8 g, female 5-2 g. Male has straight, medium-sized bill, upper mandible blackish, lower reddish with dark tip; crown glittering turquoise to violet-blue; back, rump and flanks golden green to bronze-green; centre of underparts white; undertail-coverts chiefly bronze-green with white fringes; tail greyish-green to bronze-green. Female has more turquoise reflections on crown and neck. Immature has feathers of upperparts tipped rufous; less white on underparts, belly more greyish-brown; immature male strongly resembles female in crown coloration. Race *chlorostephana* has metallic green to turquoise green crown, rarely approaching the turquoise coloration of nominate female; significantly smaller in all measurements.

Habitat. Inhabits pine and pine-oak forest, cloudforest and rainforest, edges of humid forest; also found in gallery forest, savanna, brush, abandoned fields and gardens. Races differ in altitudinal distribution; nominate race occurs regularly between 500 and 1800 m, occasionally up to 2400 m, rarely close to sea-level, for example in N Honduras. Range of race *chlorostephana* below 100 m, since tied to distribution of pine savanna (with *Pinus caribaea*); inhabits stands of pine close to gallery forest and edges of isolated evergreen rainforest.

Food and Feeding. Feeds on nectar, especially at flowering epiphytes. Hovers briefly; feeds in all strata, but mainly at 4-6 m above ground; in gallery forests, forages in streamside vegetation. Sometimes concentrates in groups at flowering *Inga* trees. Hunts aerially for insects.

Breeding. Varies with region; in Mexico, Feb-Aug; in Belize, Jan-Jul; in Guatemala, data on gonadal activity indicate Jul-Sept; in Nicaragua, breeding recorded Feb. Nest an open cup, with moss, plant fibres, pieces of lichen; placed on horizontal branch or fork, up to 15 m above ground. Clutch size 2; incubation by female; no data exist on duration of incubation or fledging.

Movements. Some populations are sedentary, for instance in Veracruz and San Luis Potosí (Mexico), whereas others are migratory. Larger numbers of wintering birds in Mexico occur along the Pacific coast of Oaxaca and Chiapas, also in the Atlantic lowlands of Guatemala and Honduras. Vagrants reach northern parts of Yucatán Peninsula. In general, altitudinal seasonality noted, with breeding ranges at higher elevations and preference for foothills and lowlands in non-breeding season.

Status and Conservation. Not globally threatened. CITES II. Common in pine and pine-oak forests of the highlands of interior Mexico, Guatemala and Honduras, rarer in cloudforest and lowland rainforest. Race *chlorostephana* of lowland pine savanna of Mosquitia, is rather uncommon and local; however, has profited from habitat alteration by man, as the decline of the original low-elevation woodlands enabled the spread of the open savanna type.

Bibliography. Anon. (1998a), Berlioz (1932b), Binford (1989), Bjelland & Ray (1977), Brown & Bowers (1985), Davis (1944, 1952), Dickey & van Rossem (1938), Edwards & Lea (1955), Friedmann *et al.* (1950), González-García (1993), Hartert (1899a), Howell, S.N.G. & Webb (1995a), Howell, T.R. (1965, 1972), Johnsgard (1997), Land (1963a, 1970), Lowery & Dalquest (1951), Martins *et al.* (1954), Monroe (1968), Phillips (1964, 1971), Rand & Traylor (1954), Ridgway (1911), Rowley (1984), Russell (1964), Siotz *et al.* (1996), Thurber *et al.* (1987), Todd (1942), Udvardy (1983), Wagner (1957b), Wetmore (1941).

153. Violet-crowned Hummingbird

Agrytria violiceps

French: Ariane à couronne violette

Spanish: Amazilia Coronivioleta

German: Veilchenscheitelamazilie

Other common names: Azurecrown, Salvin's Hummingbird

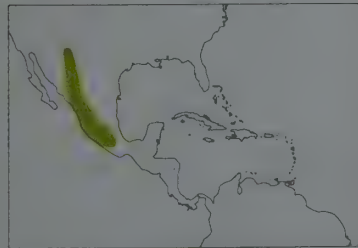
Taxonomy. *Cyanomyia violiceps* Gould, 1859, Atlitico, Puebla, Mexico.

Genus usually merged into *Amazilia*. Forms a superspecies with *A. viridifrons*, with which formerly considered conspecific. Species name sometimes given as *verticalis*, but this name refers to *A. cyanocephala*. Proposed race *conjuncta*, of Sonora, indistinguishable from *elliotti*. "*Cyanomyia salvini*", from Nacosari (Sonora), reported to be of hybrid origin with *Cyananthus latirostris*, but is probably an aberrant individual of race *elliotti*. Two subspecies recognized.

Subspecies and Distribution.

A. v. elliotti (Berlepsch, 1888) - extreme SW USA to NW & C Mexico.

A. v. violiceps (Gould, 1859) - SW Mexico.



Descriptive notes. 10 cm; 5.0 g. Male has straight, medium-sized bill, fleshy red except for dark tip; crown violet-blue; upperparts and flanks olive green to bronze-green; undertail-coverts bronze to coppery, sometimes with purplish tinge; underparts entirely white; inner rectrices bronze to purplish. Female has crown and neck more turquoise. Immature crown resembles that of female, but feathers bordered with rufous; bill more blackish above; greyish borders in rump and upperpart-coverts. Race *elliotti* has crown more turquoise bluish, the coloration extending to neck and cheeks; inner rectrices greyish golden-green.

Habitat. Inhabits semi-open to open arid scrubland, thorn forests, open pine and pine-oak forests, forest edges, riparian groves, plantations, parks and gardens. Ranges from near sea-level to 2250 m, but chiefly at 1000-1500 m.

Food and Feeding. Forages for nectar mainly in middle to upper strata; recorded for example at *Agave*. Insects are caught in the air by hawking.

Breeding. Mainly Apr-Aug, but nesting and birds in breeding condition have been observed until Jan. Cup-like nest, consisting of plant material such as cotton-like fibres and green lichen, fixed with cobweb; usually placed on dead twig, horizontal branch or tip of overhanging branch. In Guadalupe Canyon, USA, nests found at heights of 7-12 m in sycamore trees (*Platanus wrightii*); nests in Mexico located in shrubs or small oak trees 1-2 m above ground. Clutch size 2; incubation by female; no data exist on incubation and fledging periods.

Movements. Partially migratory. Northernmost populations probably winter along N Pacific slope from SE Sonora southward, and on Atlantic slope from Guanajuato to Hidalgo; earliest summering birds in Sonora can be observed regularly in Mar, although there are indications of overwintering individuals. Representatives of race *violiceps* mostly occur in winter along the S Pacific slope from Guerrero to Oaxaca; latest summering individuals reported in October. Recent spring and breeding season records from California indicate overwintering birds or even migrational trends that could establish a new breeding population in W USA.

Status and Conservation. Not globally threatened. CITES II. Common to uncommon resident throughout range. Race *elliotti* occurs very locally in SE Arizona and SW New Mexico, where confined to the riparian vegetation of Guadalupe Canyon; rarely found in NE Sonora, more common in southern parts of range. Nominative race is a more frequent breeder in the interior parts of SC Mexico than in the coastal regions.

Bibliography. Anon. (1998a), Baicich & Harrison (1997), Baltosser (1986a, 1989b), Bent (1940), Berlioz (1932a, 1932b), Binford (1989), Bishop (1906), Brewster (1893), Cisneros & Bonilla (1993), Davis (1944), DeGraaf & Rappole (1995), Des Granges & Grant (1980), Edwards & Lea (1955), Eguarte *et al.* (1987), Friedmann *et al.* (1950), Gray (1958), Hartert (1899a), Howell & Webb (1995a), Johnsgard (1997), Johnson, J.A. & Ziegler (1978), Johnson, T.B. (1987), Johnston & Hardy (1959), Kaufman (1996), Lasiewski & Lasiewski (1967), Levy (1958), Ligon (1961), McCaskie (1976, 1987), Phillips (1964), Ridgway (1911), Rising (1965), van Rossem (1945a), Rowley (1966), Selander & Giller (1959), Sheppard (1968), Short (1974), Simon (1911), Storer (1961), Stotz *et al.* (1996), Stresemann (1954), Wagner (1957a), Wetmore (1943), Yee *et al.* (1992), Zimmerman & Levy (1960).

154. Green-fronted Hummingbird

Agrytria viridifrons

French: Ariane à front vert

German: Grünscheitelamazilie

Spanish: Amazilia Freniverde

Other common names: Cinnamon-sided Hummingbird (*wagneri*)

Taxonomy. *Cyanomyia viridifrons* Elliot, 1871, Putla de Guerrero, Mexico.

Genus usually merged into *Amazilia*. Forms a superspecies with *A. violiceps*. Until mid-20th century, holotype of present species was believed to represent an aberrant individual of *A. violiceps*, due to sexual and age-related variation in coloration of crown in both species; in addition, forms described as "*Cyanomyia guerrensis*", "*Uranomitra dermeddei*" and "*U. atricapilla*" all refer to present species but were earlier considered synonyms of *A. violiceps*; when finally recognized as a valid taxon, present species was considered a race of *A. violiceps*; recent morphological and biogeographical studies, however, including discovery of zone of sympatry in Guerrero but no known hybridization, confirm validity of present species. Race *wagneri* sometimes considered a separate species, but morphological differences slight. Birds from C Oaxaca have been awarded race *rowleyi*, but probably not valid, due to strong intergradation of nominate and race *wagneri* in zone of supposed secondary contact. Nominative race shows disjunct distribution, with gap in E Oaxaca. Two subspecies recognized.

Subspecies and Distribution.

A. v. viridifrons (Elliot, 1871) - S Mexico: E Guerrero to W Oaxaca; E Oaxaca to C Chiapas.

A. v. wagneri (Phillips, 1964) - S Mexico: C & S Oaxaca.



Descriptive notes. 10-11.5 cm; 5.5 g. Male has straight, medium-sized bill, flesh red with dark tip; crown dark-coloured, appears blackish from a distance but glittering oily to bluish-green close up; nape, mantle and sides of breast emerald to bronze-green; rump and upperpart-coverts greyish-brown to bronze; chin, throat and centre of belly white; flanks bronze-green, sometimes with pale cinnamon to vinaceous spots; undertail-coverts white, centres often with cinnamon to vinaceous spots or streaks; rectrices coppery to purplish, edged with bronze-green. Female has crown dark green; tail less coppery, bronze to gold-green. Immature shows pale cinnamon feather tips on upperparts and rectrices; immature male has crown coloration similar to female. Race *wagneri* has cinnamon flanks and sides, and cinnamon-rufous bases to secondaries and inner primaries.

Habitat. Resident of temperate arid to semi-arid, open pine-oak forest, oak scrub, thorn forest; sometimes found at edges of humid forest, in riparian woodland, parks and gardens. Western population of the nominate race recorded between 730 and 1400 m, whereas eastern population found down to 60 m; race *wagneri* ranges from 250 to 900 m.

Food and Feeding. Forages for nectar at flowering bushes and trees from middle to upper strata; diet includes small insects which are caught by hawking.

Breeding. Data on nesting and gonadal activity from Oaxacan birds indicate Dec-May, Aug-Oct; for Chiapas, at least Apr-Jun. Nest cup-shaped, made of plant-wool and lichen, fixed with cobweb, 2-3 m above ground. Clutch size 2, eggs often appearing stained due to washing out of nest material by rain; incubation by female; no further information available.

Movements. Generally sedentary with some local movements, as indicated by altitudinal shifts in distribution of post-breeders towards lower elevations. Nominative birds may occasionally occur along the Atlantic coast of Yucatán as indicated by one record from Belize. Status in extreme W Guatemala uncertain, but species may be resident.

Status and Conservation. Not globally threatened. CITES II. Fairly common in the arid tropical zone of the Sierra Madre del Sur and the Sierra Madre de Chiapas. In Guerrero, mainly found in Rio Balsas drainage; in Oaxaca, mostly recorded from Rio Grande drainage, but also found in tributaries of Rio Verde, and S of Sierra de Miahuatlán. Eastern population of nominate *viridifrons* is common resident from Pacific slope foothills of extreme E Oaxaca to interior Chiapas (Grijalva Valley), but apparently absent from Pacific slope of Sierra Madre de Chiapas.

Bibliography. Anon. (1998a), Berlioz (1932b), Binford (1989), Davis (1972), Friedmann *et al.* (1950), Hartert (1899a), Howell (1993c), Howell & Webb (1995a), Johnsgard (1997), Phillips (1964), Ridgway (1911), Rowley (1966, 1984), Schuchmann (1990b), Simon (1911), Stotz *et al.* (1996), Wetmore (1947).



Genus *POLYERATA* Heine, 1863

155. Glittering-throated Emerald

Polyerata fimbriata

French: Ariane de Linné **German:** Glitzerkehlamazilie **Spanish:** Amazilia Listada

Taxonomy. *Trochilus fimbriatus* J. F. Gmelin, 1788, Cayenne.

Genus sometimes lumped into *Agyrtia*; these two usually merged into *Amazilia*. Forms a superspecies with *P. lactea*. Races *fluvialis*, *nigricauda* and *tephrocephala* were all previously treated as distinct species. Several proposed races are invalid due to similar morphology and range overlap with adjacent forms: *obscuricauda* has proved to be identical to *elegantissima*; *maculicauda* and *alia* are inseparable from nominate race. In Táchira, Venezuela, the very local "*Amazilia distans*" is most probably of hybrid origin, present species x *Hylocharis cyanus*. "*P. cyaneotincta*", known only from two skins of uncertain origin, has been suggested to be aberrant form of present species, but this seems unlikely; in plumage pattern more similar to *P. amabilis*. Seven subspecies currently recognized.

Subspecies and Distribution.

P. f. elegantissima (Todd, 1942) - extreme NE Colombia and N & NW Venezuela.

P. f. fimbriata (J. F. Gmelin, 1788) - NE Venezuela from Orinoco basin to the Guianas and N Brazil N of Amazon.

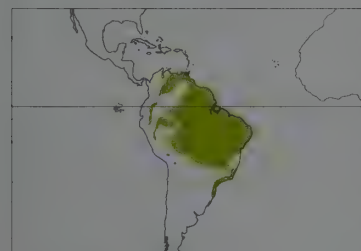
P. f. apicalis (Gould, 1861) - Colombia E of Andes.

P. f. fluvialis (Gould, 1861) - SE Colombia and E Ecuador.

P. f. laeta (Hartert, 1900) - NE Peru.

P. f. nigricauda (Elliot, 1878) - E Bolivia and C Brazil S of Amazon.

P. f. tephrocephala (Vieillot, 1818) - coastal SE Brazil from Espírito Santo to Rio Grande do Sul.



Descriptive notes. 8-12 cm; 4-6 g. Male has straight, medium-sized bill, upper mandible blackish, lower pinkish, tipped dark; upperparts golden to bronze-green; throat and breast glittering golden green, rarely with turquoise sheen; centre of lower breast, belly white; undertail-coverts white with brownish centres; tail dark bronze-green to blackish-bronze. Female with white subterminal bars on throat feathers; outermost rectrices have greenish-grey tips. Immature has whitish on belly reduced, more greyish-brown. Race *elegantissima* has coppery to purplish upperpart-coverts; *apicalis* has significantly longer bill; *fluvialis* and *laeta* show turquoise to bluish sheen on throat, and *fluvialis* has significantly longer bill; *nigricauda* and *tephrocephala* have pure white undertail-coverts and greenish-black to bluish-black tail; *tephrocephala* is slightly heavier, and significantly larger in all morphometric characters.

Habitat. Generally widespread in open to semi-open areas; normally absent from interior of dense forest. Present in a great variety of habitats, including dry and humid forests, forest edges, gallery forest, second growth, open woodland, savanna, scrub, plantations and gardens. In central parts of Brazil, a typical bird of the *caatinga* and *capoeira*; also inhabits mangroves along the Atlantic coast. Ranges from sea-level to 1100 m, mainly below 500 m.

Food and Feeding. Mostly feeds in lower strata of flowering trees, often close to ground, and takes nectar also while perching; trap-liner. Forages for nectar at a great variety of native and introduced plant families and species, among them Bromeliaceae, Leguminosaceae, Passifloraceae, Heliconiaceae, Malvaceae, Proteaceae, Cactaceae and Rubiaceae; in gardens, often at flowering herbs and bushes, such as *Malvaviscus*, *Azibulon*, *Genipa*, or *Stachytarpheta*, trees like *Inga* and *Citrus*, or climbers like *Thunbergia*. Also hunts for insects such as small flies (Diptera) and beetles.

Breeding. Almost all year round; in Guyana and NE Brazil, data indicate Aug-Sept, in Argentina, Paraguay and Uruguay Nov-Dec. Nest cup-shaped, placed on horizontal branch, rarely in fork; consists of plant wool, cobweb, lichen; usually found low down, mostly below 4 m, sometimes less than 1 m, occasionally up to 8 m. One nest of race *nigricauda* was placed in a shrub, and made of *Typha* and Bromeliaceae kopak and compound leaves. Nest-building takes 6-12 days. Clutch size 2; incubation 14-17 days, by female; chick darkish, with sparse buff dorsal down; fledging at 18-22 days. Two broods or more possible per year.

Movements. Race *tephrocephala* migrates regularly southward along Atlantic coast, occasionally reaching Rio Grande do Sul. Other races probably make only very local movements, though not well known.

Status and Conservation. Not globally threatened. CITES II. Common to very common in many parts of the range, especially within northern and eastern regions. Has been erroneously reported once from Trinidad. Current distributional limits of populations E of Andes from Venezuela to Peru poorly known. Race *tephrocephala* is locally common breeder in SE Brazil, but generally uncommon along Atlantic coast; despite its occupation of open areas, species has presumably suffered from destruction of coastal forest. Form "*distans*", probably of hybrid origin, has been classed as Endangered.

Bibliography. Alves & Cavalcanti (1996), Belton (1984), Berger & Hart (1972), Berlioz (1929a, 1934), Bloch *et al.* (1991), Bond & Meyer de Schauensee (1943), Cintra & Yamashita (1990), Collar *et al.* (1992), Cotton (1998a), Friedmann (1948), Friedmann & Smith (1950, 1955), Grantsau (1988), Graves (1998), Griscom & Greenway (1941), Havenschnudt (1952a, 1952b, 1958a), Havenschnudt & Mees (1994), Hellmayer (1907, 1929), Hilty & Brown (1986), Jouanin (1948), Mayr (1971), Meyer de Schauensee (1959, 1964), Meyer de Schauensee & Phelps (1978), Nicéforo & Olivares (1967), Oniki (1996), Parker *et al.* (1982), Ricklefs (1968), do Rosário (1996), Ruschi (1949a, 1950b, 1976d, 1981-1982, 1986), Rutgers & Norris (1972), Sánchez (1995), Schäfer (1952), Schuchmann & Bosque (1988), Sick (1993, 1997), Sick & Pabst (1968), Sick & Teixeira (1981), Simón (1921), Sneath (1928a, 1928b), Snyder (1966), Stotz *et al.* (1996), Thomas (1993), Todd (1942), Tostain *et al.* (1992), Wege & Long (1995), Weiss-Fogh (1972), Weller & Schuchmann (1997), Wetmore (1939), Wetmore & Phelps (1956), Willis (1992), Zimmer (1950f), Zimmer & Phelps (1951).

156. Sapphire-spangled Emerald

Polyerata lactea

French: Ariane saphirine **German:** Saphiramazilie **Spanish:** Amazilia Zafirina
Other common names: Tepui Emerald (*zimmeri*); Bartlett's Emerald (*bartletti*)

Taxonomy. *Ornismya lactea* Lesson, 1832, the Guianas and Brazil.

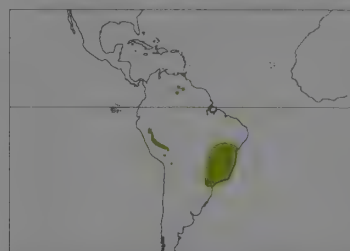
Genus sometimes lumped into *Agyrtia*; these two usually merged into *Amazilia*; present species has alternatively been placed in *Hylocharis*. Forms a superspecies with *P. fimbriata*. The three races show highly disjunct distribution; race *bartletti* sometimes treated as a separate species; *zimmeri* too has been more tentatively suggested as sufficiently distinctive to merit splitting as a further species. Three subspecies currently recognized.

Subspecies and Distribution.

P. l. zimmeri (Gilliard, 1941) - SE Venezuela.

P. l. bartletti (Gould, 1866) - E & SE Peru and N Bolivia; doubtfully extreme E Ecuador.

P. l. lactea (Lesson, 1832) - C & S Brazil from S Bahia to São Paulo.



Descriptive notes. 8-11 cm; male 4-0 g, female 3-6 g. Male has straight, medium-sized bill, upper mandible blackish, lower pinkish to horn-coloured with greyish tip; crown, neck, and flanks bronze-green; rest of upperparts golden to bronze-green; throat, upper breast glittering violet-blue; centre of breast white, belly greyish, undertail-coverts whitish with brown basal streak; median rectrices basally shining green, laterally as outer rectrices bluish-black. Female has throat more greyish, with discs rather glittering turquoise than violet; outermost rectrices with greyish tips. Immature has extended greyish areas on underparts; immature male resembles adult female in throat coloration. Race *zimmeri* is distinguished by reduction of violet patch on throat, with greyish-fringed feathers; *bartletti* is characterized by longer bill and wings, more conspicuous greyish fringing on throat, greenish centre of belly, below greyish, undertail-coverts with prominent brown centres.

Habitat. Inhabits edges of rainforest, gallery forest, second growth and clearings; particularly in south of range often found in open to semi-open habitats such as *capoeiras*, parks, orchards, gardens, etc. Normally occurs below 1000 m, rising to 1400 m in Pantepui area of Venezuela and submontane zone of Peruvian Andes; Brazilian population close to sea-level.

Food and Feeding. Forages for nectar at a great variety of native and introduced plants; some preferred plant families are Leguminosaceae, Malvaceae, Heliconiaceae and Rubiaceae. In parks and suburban areas often found at flowering shrubs and trees, such as *Inga*, *Citrus*, *Eucalyptus*, or *Genipa*. Male establishes feeding territory. Insects are caught in the air by hawking.

Breeding. Southern populations breed Oct-Jan at least; season of Venezuelan birds unknown. Nest cup-shaped, built of plant down, cobweb, outside covered with lichens. One nest in Bolivia constructed 2 m up in papaya tree. Clutch size 2; incubation 14 days, by female; chick darkish, with some buff dorsal down; fledging period 22 days.

Movements. Southern populations are short-distance migrants; nothing is known on movements of northern population.

Status and Conservation. Not globally threatened. CITES II. Common to very common in western and eastern parts of range notably in Brazil, where occurs in several protected areas, e.g. Serra dos Órgãos and Itatiaia National Parks (Rio de Janeiro) and Serra do Cipó National Park (Minas Gerais). Current distribution and population size in Venezuela requires confirmation, where race *zimmeri* is very local and disjunct in range and known only from three collecting sites in Bolívar, the northernmost, Auyán Tepui, is located in Canaima National Park.

Bibliography. dos Anjos *et al.* (1997), Berlepsch & Stolzmann (1902), Berlioz (1965), Bond & Meyer de Schauensee (1943), Boucard (1892a), Brace *et al.* (1997), Cintra & Yamashita (1990), Donahue (1994), Gilliard (1941), Grantsau (1988), Gyldenstolpe (1945b), Meyer de Schauensee (1966), Meyer de Schauensee & Phelps (1978), Niethammer (1953), Oniki (1996), Parker *et al.* (1982), Remsen & T aylor (1989), do Rosário (1996), Ruschi (1949a, 1953b, 1981-1982, 1986), Sánchez (1995), Sick (1993, 1997), da Silva (1996), Snow & Teixeira (1982), Stotz *et al.* (1996), Terborgh *et al.* (1984), Willis (1992), Zimmer (1950f).

157. Blue-chested Hummingbird

Polyerata amabilis

French: Ariane aimable **German:** Blaubrustamazilie **Spanish:** Amazilia Amable
Other common names: Blue-breasted/Beryl-crowned/Lovely Hummingbird; Charming Hummingbird (*decora*)

Taxonomy. *Trochilus* (—?) *amabilis* Gould, 1853, Colombia.

Genus sometimes lumped into *Agyrtia*; these two usually merged into *Amazilia*. Race *decora* sometimes considered a separate species, on grounds mainly of morphological differences, combined with distribution. Proposed race *costaricensis* (Nicaragua to Panama) inseparable from nominate. Two subspecies recognized.

Subspecies and Distribution.

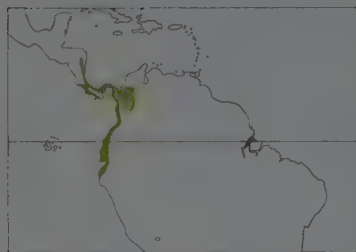
P. a. amabilis (Gould, 1853) - NE Nicaragua to NC Colombia and Ecuador W of Andes; possibly SE Honduras.

P. a. decora Salvin, 1891 - Pacific slope from SW Costa Rica to W Panama.

Precise limits of range uncertain in NE Nicaragua and S Ecuador, and perhaps elsewhere.

Descriptive notes. 7-11 cm; male 4-1 g, female 3-8 g. Male has straight, medium-sized, blackish bill, lower mandible basally reddish; crown and malar area glittering green with slight bluish tinge; upperparts and flanks dull green to bronze-green; chin centrally bronzy; lower throat and breast with violet-blue patch and greyish-edged discs; lower belly greyish-brown; undertail-coverts with brownish centres; upperpart-coverts and tail bronze-green, rarely dull green, with some purplish reflections in the tail-coverts and median rectrices; outer rectrices becoming blackish. Female lacks glittering crown; instead of distinct throat patch has scattered turquoise to bluish feathers with

On following pages: 158. Purple-chested Hummingbird (*Polyerata rosenbergi*); 159. Mangrove Hummingbird (*Polyerata boucardi*); 160. Honduran Emerald (*Polyerata luciae*); 161. Steely-vented Hummingbird (*Saucerottia saucerottiei*); 162. Indigo-capped Hummingbird (*Saucerottia cyanifrons*); 163. Snowy-breasted Hummingbird (*Saucerottia edwardi*); 164. Blue-tailed Hummingbird (*Saucerottia cyanura*); 165. Berylline Hummingbird (*Saucerottia beryllina*); 166. Green-bellied Hummingbird (*Saucerottia viridigaster*); 167. Copper-tailed Hummingbird (*Saucerottia cupreicauda*); 168. Copper-rumped Hummingbird (*Saucerottia tobaci*).



broad whitish margins; belly paler; rectrices with greyish tips. Immature resembles female in throat coloration but more greyish in underparts. Race *decora* has longer bill and wings; glittering green of crown extends further back towards nape, upperparts average duller.

Habitat. Inhabits forest edges, open woodland, thickets, second growth, clearings, riparian vegetation, plantations, etc.; visits gardens with flowering trees. Generally commoner in open areas; avoids interior of dense forest. Occurs from sea-level to 1400 m; nominate race normally below 500 m and infrequent above 1000

m; race *decora* prefers lowlands as well as sub-montane zones of the slopes of Cordillera de Talamanca and Cordillera Central, and is encountered more often at medium elevations than nominate.

Food and Feeding. Forages for nectar, usually in lower strata at herbs such as *Heliconia* and shrubs; occasionally higher up in middle strata. In Colombia, recorded at diverse tree species, including *Inga*, *Bravasia* and *Hamelia*. Feeds by trap-lining or defends feeding territories that are different from those established during courtship.

Breeding. In Costa Rica, nesting starts with dry season from Dec to May; similar season assumed for Panama and Colombia. Cup-shaped nest on horizontal, leafy branch, in bush or small tree 2-5 m above ground; fixed with light-coloured plant fibres and cobweb; inside sometimes covered with seed-down and brown fern scales, outside with lichen and moss. Clutch size 2; incubation by female; chick flesh-coloured, with sparse buff dorsal down; no data exist on incubation and fledging periods.

Movements. Short-distance migrant; movements partially correlated with flowering period. Seasonal movements appear erratic, as individuals suddenly appear or disappear in certain places. May occur at higher altitudes after breeding season.

Status and Conservation. Not globally threatened. CITES II. Relatively common, at least locally, in most parts of range. One of the commonest trochilids in the Canal Zone. Race *decora* sometimes considered full species and classified as restricted range species: present in South Central American Pacific Slope EBA; in Costa Rica, this race occurs in several protected areas, e.g. Manuel Antonio and Corcovado National Parks and Golfito National Wildlife Refuge.

Bibliography. Bertin & Wilzbach (1979), Blake & Loisel (1991), Brosset (1964), Butler (1932a, 1932b), Eudes-Deslongchamps (1881), Gill *et al.* (1982), Gray (1958), Haffer (1975), Hartert (1898), Hilty (1985), Hilty & Brown (1986), Howell (1957), Karr (1977), Marcus (1983), Ridgely & Gwynne (1989), Rutgers & Norris (1972), Salaman & Mazariegos (1998b), Skutch (1958, 1966, 1972), Slud (1964), Stiles (1980, 1995b), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968a), Williams & Tobias (1994), Willis & Eisenmann (1979).

158. Purple-chested Hummingbird

Polyerata rosenbergi

French: Ariane de Rosenberg **German:** Rosenbergamazilie **Spanish:** Amazilia de Rosenberg
Other common names: Rosenberg's Emerald

Taxonomy. *Polyerata rosenbergi* Boucard, 1895, Río Dagua, Colombia.

Genus sometimes lumped into *Agyrtia*; these two usually merged into *Amazilia*. Proposed race *reini* (NW Ecuador) separated on basis of extent of breast patch, different throat coloration and longer bill, but these traits are attributable to individual variation. Monotypic.

Distribution. W Colombia and NW Ecuador.



Descriptive notes. 8-10 cm; male 4.0 g, female 3.5 g. Male has straight, medium-sized bill, upper mandible blackish, lower fleshy red except for dark tip; upperparts golden to dark golden green; uppertail-coverts bronze-green to purplish; underparts golden green, with violet-blue patch on upper breast; belly brownish, undertail-coverts pure white; central rectrices bronze to purple-green, outer rectrices more blackish-green. Female lacks the breast patch but exhibits an indistinct band of turquoise to bluish feathers with whitish margins; belly paler greyish; rectrices tipped white. Immature resembles female in throat-patch coloration.

Habitat. Rainforest, forest edges, second growth and clearings; occurs from near sea-level to 200 m. **Food and Feeding.** Forages for nectar at a great variety of plants, and feeding has been recorded from *Costus*, *Heliconia*, Ericaceae (*Macleania*, *Psammisia*), Gesneriaceae (*Allopectus*, *Besleria*, *Drymonia*, *Gasteranthus*) and Loranthaceae (*Tristerix*).

Breeding. Jan-Apr. Nest tiny, cup-shaped, made of soft plant fibres and lichen; built in low trees and vines, 2-4 m above ground. Clutch size 2; incubation 15-17 days, by female; chick darkish, with some buff dorsal down; fledging at 20-24 days.

Movements. Some local dispersal, but movements poorly understood.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Chocó EBA. Locally common resident. In coastal SW Colombia, recorded density of at least 2-3 pairs/km². Present in Río Nambi Reserve, Colombia.

Bibliography. Best *et al.* (1997), Butler (1979), Chapman (1917, 1926), Hartert (1898), Hellmayr (1911), Hilty & Brown (1986), Meyer de Schauensee (1982), Olrog (1968), Salaman & Mazariegos (1998b), Stotz *et al.* (1996).

159. Mangrove Hummingbird

Polyerata boucardi

French: Ariane de Boucard **German:** Mangrovenamazilie **Spanish:** Amazilia de Manglar
Other common names: Boucard's Hummingbird

Taxonomy. *Arena Boucardi* Mulsant, 1877, Puntarenas, Costa Rica.

Genus sometimes lumped into *Agyrtia*; these two usually merged into *Amazilia*; species alternatively placed in *Lepidopyga*. Forms a superspecies with *P. luciae*. Monotypic.

Distribution. Pacific coast of Costa Rica from Gulf of Nicoya to Gulf of Dulce.

Descriptive notes. 10-11 cm; 4-5 g. Male has slightly decurved, medium-sized bill, upper mandible blackish, lower reddish, distally dusky grey; upperparts and flanks golden to bronze-green; throat and breast glittering bluish-green, feathers towards chin with prominent white subterminal



bars; belly whitish, with bronze-green sides; undertail-coverts white; tail slightly forked, with almost blackish lateral and terminal portions on outer rectrices. Female white below, sides of throat spangled with some bluish-green spots; outermost rectrices with greyish tips. Immature male resembles female in throat coloration; more greyish below than adult.

Habitat. Chiefly mangroves with extensive stands of Pacific mangrove (*Pelliciera rhizophorae*), and sometimes in neighbouring second growth, often on sandbars; exclusively at or close to sea-level.

Food and Feeding. Nectar of various native and introduced plants; in addition to *Pelliciera*, visits adjoining vegetation including trees like *Lonchocarpus*, epiphytes and vines. Hunts aerially for mosquitoes.

Breeding. Oct-Feb. Nest has form of a small cup; consists of balsa floss, plant down, cobweb, with lichens on outside wall; usually placed on mangrove twigs, overhanging water, 1-4 m up. Clutch size 2; incubation by female; no data exist on duration of incubation or fledging.

Movements. Sedentary.

Status and Conservation. VULNERABLE. CITES II. Restricted-range species: present in South Central American Pacific Slope EBA. Still locally common. Recent decline caused by destruction of mangrove habitat by establishment of salinas and shrimp ponds, road construction and illegal wood cutting. For survival or recovery of remnant populations suitable areas should be protected and existing reserves extended. Generally, still insufficiently protected; for example, the Biological Reserve of Tivives contains only a relatively small amount of *Pelliciera*. Other localities where species occurs include mangroves between the mouths of the rivers Pirris and Palo Seco, Carara Biological Reserve and Golfito Faunal Refuge. Survey of abundance in presumed but still unexplored breeding habitats is necessary to evaluate the current status of the species.

Bibliography. Alfaro (1935), Anon. (1998a), Boucard (1878), Carraker (1910), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Cory (1918), Slud (1964, 1980), Stattersfield *et al.* (1998), Stiles (1985c), Stiles & Skutch (1989), Stotz *et al.* (1996), Wege & Long (1995).

160. Honduran Emerald

Polyerata luciae

French: Ariane de Lucy **German:** Hondurasamazilie **Spanish:** Amazilia Hondureña
Other common names: Honduras/Lucy's Emerald

Taxonomy. *Thaumatias Luciae* Lawrence, 1867, Honduras.

Genus sometimes lumped into *Agyrtia*; these two usually merged into *Amazilia*. Forms a superspecies with *P. boucardi*. Monotypic.

Distribution. Arid interior valleys of N & C Honduras.



Descriptive notes. 9-10 cm. Male has straight, medium-sized bill, upper mandible blackish, lower reddish, distally dusky; upperparts golden green, towards tail-coverts more bronze; throat and breast glittering turquoise to blue-green; flanks greenish, belly with greyish centre; undertail-coverts with white borders and brownish centre; tail slightly forked, light bronze-green, with purplish-black subterminal band on the outer rectrices. Female has throat less intensely turquoise with more greyish areas; grey tips to outer rectrices. Immature resembles female in throat coloration, but has more buff-coloured rectrice tips.

Habitat. Inhabits arid thorn forest, scrub and open woodland, from 75 m to 300 m.

Food and Feeding. Perches and feeds in low to fairly high strata, at 0.5-10 m above ground. Forages for nectar at various flowering plants, such as *Pithecellobium*, *Aechmea*, *Pedilanthus* and Cactaceae. Hunts aerially for insects.

Breeding. Birds in breeding condition observed in June; nesting unknown. Clutch size 2; incubation by female; no data exist on incubation and fledging periods.

Movements. No information available.

Status and Conservation. CRITICALLY ENDANGERED. CITES II. One of the most threatened trochilids. Until its rediscovery in 1988, biology and status were almost unknown, and the taxon was even believed to be extinct. Apparently still locally common; most of recently recorded localities are restricted to upper Aguán Valley; population discovered in Agalta Valley in 1996, where present species was commonest hummingbird, but already threatened by active destruction of habitat for agriculture and grazing. As with *P. boucardi*, the major threat is rapidly increasing habitat destruction; particularly areas with thorn forest have been widely cleared, to be either converted into plantations, especially of pineapples, or used as pasture. Nevertheless, the species seems to tolerate some disturbance, such as grazing, as long as its preferred habitat still survives. Current status of relict populations requires more intensive study, in terms of both population size and range. Conservation measures, chiefly protection of suitable habitats, are urgently required to ensure survival of this species.

Bibliography. Anderson *et al.* (1998), Anon. (1989a, 1998a), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Greenway (1978), Howell & Webb (1989, 1992a, 1995a), Monroe (1968), Moore (1938), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Wege & Long (1995).

Genus SAUCEROTTIA Bonaparte, 1850

161. Steely-vented Hummingbird

Saucerottia saucerrottei

French: Ariane de Sophie **German:** Stahlgrüne Amazilie **Spanish:** Amazilia Verdiazul
Other common names: Saucerotte's/Blue-vented Hummingbird

Taxonomy. *Trochilus saucerrottei* DeLattre and Bourcier, 1846, Cali, Colombia.

Genus usually merged into *Amazilia*. Forms a superspecies with *S. cyanifrons*. Proposed race *australis* described from small series of specimens from Guaitara Valley (SW Colombia) on basis of morphometric differences from nominate; however, strong clinal variation within larger series of nominate birds indicates that it should not be retained. Remarkably isolated race *hoffmanni* sometimes considered to represent a distinct species on basis of behaviour and voice, in addition to distribution; this taxon formerly listed as *S. sophiae*. Four subspecies recognized.

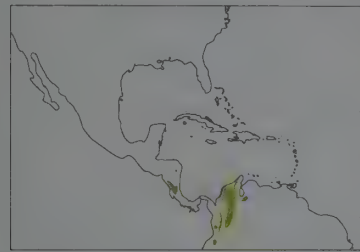
Subspecies and Distribution.

S. s. hoffmanni (Cabanis & Heine, 1860) - W Nicaragua and W & C Costa Rica.

S. s. warszewiczi (Cabanis & Heine, 1860) - N Colombia and extreme NW Venezuela.

S. s. braccata (Heine, 1863) - W Venezuela (Andes of Mérida and Trujillo).

S. s. saucerrottei (DeLattre & Bourcier, 1846) - NW, N & W Colombia.



Descriptive notes. 8-11 cm; male 5.0 g, female 4.5 g. Male has straight, medium-sized bill, upper mandible blackish, lower coral red with dark tip; upperparts golden green; underparts glittering dark golden green; undertail-coverts greenish to steel blue; uppertail-coverts and rectrices blue-black; tail slightly forked. Female similar but differs in white subterminal bars on throat feathers, more greyish-brown undertail-coverts, less forked tail. Immature shows dull green, partially dark grey throat; brownish borders to feathers on back and rump; greyish-brown belly. Race *hoffmanni* has rump and uppertail-coverts coppery to purplish,

rectrices lighter, steel blue; *warszewiczi* has purplish to bluish tinge in uppertail-coverts, smaller in all morphometric characters than all other races; *braccata* often has rump feathers tipped purplish, uppertail-coverts violet-blue to bluish.

Habitat. In general, inhabits open to semi-open, scrubby areas, savannas, forest edges, second growth, plantations, gardens, etc. Normally found in relatively arid habitats, for example N Colombian and Caribbean dry forests, but in dry season also prefers wetter areas like edges of gallery forest. Ranges from sea-level to at most 1500 m; Venezuelan race *braccata* mainly around 2000m, rarely up to 3000 m.

Food and Feeding. Forages at nectar-producing flowers in low bushes and trees, where often becomes territorial. Recorded at great variety of plants, including trees such as *Inga*, *Tabebuia*, or *Genipa*, shrubs like *Hamelia* and *Stachytarpheta*, herbs (*Lobelia*), vines and epiphytes. Feeds also on insects that are sometimes taken from water surface.

Breeding. Almost all year round. In Colombia, birds in breeding condition or nests have been found Jan-Oct; in Costa Rica, Dec-Apr. Small, cup-like nest, made of light-coloured plant down and cobweb, decorated on outside with lichen; built on branch or twig of smaller tree, 2-8 m above ground. Clutch size 2; incubation by female; no further information available.

Movements. Some local dispersal; seasonally abundant in areas with flowering plants.

Status and Conservation. Not globally threatened, CITES II. Fairly common to locally common in more arid regions. Costa Rican population of *hoffmanni* has apparently profited from deforestation and spread of plantations as indicated by recent invasion into the valleys of the central plateau; nevertheless, still uncommon to rare along the Caribbean slope; this race occurs in several protected areas such as Santa Rosa, Palo Verde and Barra Honda National Parks, Costa Rica.

Bibliography. Borrero (1972), Cory (1918), Darlington (1931), Feinsinger (1976, 1977, 1980), Feinsinger & Colwell (1978), Fjeldså & Krabbe (1990), Hellmayr (1913), Hilty & Brown (1986), Meyer de Schauensee (1951), Meyer de Schauensee & Phelps (1978), Miller (1963), Sánchez (1995), Slud (1964, 1980), Stiles (1985b), Stiles & Skutch (1989), Stiles & Wolf (1970), Stotz *et al.* (1996), Tiebout (1989, 1991a, 1991b, 1992, 1993, 1996), Tiebout & Nagy (1991), Trombulak (1983, 1990), Wolf (1970).

162. Indigo-capped Hummingbird

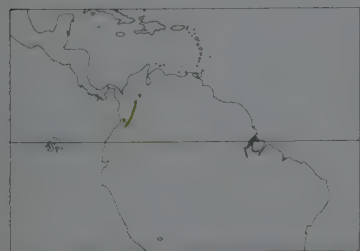
Saucerottia cyanifrons

French: Ariane à front bleu **German:** Blaukappenamazilie **Spanish:** Amazilia Capiazul
Other common names: Blue-capped/Blue-fronted Hummingbird

Taxonomy. *Trochilus cyanifrons* Bourcier, 1843, Ibagué, Colombia.

Genus usually merged into *Amazilia*. Forms a superspecies with *S. saucerrottei*. A certain amount of taxonomic confusion has resulted mainly from occurrence of differing phenotypes. The status of *S. alfarouana* from Volcán de Miravalles (Costa Rica) has been the subject of controversy due to its unusual turquoise blue cap, among other features; since a hybrid origin is most unlikely for phenotypical reasons, more recent opinion suggests that the unique type represents a race of present species; however, other morphological characters, including size, place *alfarouana* close to *S. saucerrottei* as well, so specific status should not be rejected; nevertheless, considering the lack of recent records, *S. alfarouana* should probably be regarded as extinct. A melanistic variety formerly called "Eriocnemis incultus" or "S. nunezi" refers to present species; the specimens concerned have also been erroneously considered aberrant individuals of *S. viridigaster*. Monotypic.

Distribution. N & C Colombia.



Descriptive notes. 7-10 cm; 5.0 g. The only member of the genus that shows a contrasting cap. Male has straight, medium-sized, blackish bill, with basal third of lower mandible fleshy red; crown indigo blue; upperparts shining green with bronze to coppery gloss on rump; underparts glittering golden green; undertail-coverts bordered whitish, coloration of feather centres varying from bronze-green to dark brownish or bluish; uppertail-coverts with bronze or copper tinge, becoming dark blue to bluish-black towards tail; tail slightly forked, rectrices glittering deep steel blue. Female fairly similar but crown more turquoise blue towards the neck;

throat feathers with greyish subterminal bars. Immature resembles female in crown; belly greyer.

Habitat. Edges of subtropical wet forest as well as drier, open habitats with bushes; also found in plantations and gardens. Commonest between 1000 and 2000 m, but down to 400 m in breeding season; rarely up to 3000 m. Post-breeding birds occur occasionally in tropical lowlands at sea-level.

Food and Feeding. Forages for nectar and small arthropods at various heights, but usually in upper strata. Sometimes gathers in some numbers at flowering trees. Recorded feeding plants are trees

and shrubs such as *Eugenia* and *Hamelia* and epiphytes like *Guzmania*; prefers solitary trees. Hunts for insects in the more open canopy region by sallying from perches; rarely gleans arthropods from leaves. Territorial, defending feeding places against other trochilids or nectarivorous species like Bananaquit (*Coereba flaveola*); dominance over *Agyrtia franciae* has been observed.

Breeding. Data on gonadal activity indicate season probably Apr-Jul; nest-building also recorded until Aug. Nest resembles that of congeners; cup-like, made of moss, lichens and cobweb. Clutch size 2; incubation by female; no data exist on duration of incubation or fledging.

Movements. Occasional occurrence in the Pacific lowlands suggests altitudinal migration tied to seasonal availability of food plants.

Status and Conservation. Not globally threatened, CITES II. Generally uncommon to locally common resident of semi-open woodland. Status not well known, but wide altitudinal range, combined with apparent adaptability to man-made habitats, suggests species relatively secure at present.

Bibliography. Berlioz (1937), Cory (1918), Elliot (1889), Furness (1979), Greenway (1978), Hilty & Brown (1986), Meyer de Schauensee (1982), Munves (1975), Olrog (1968), Schuchmann (1979e), Slud (1964), Snow & Snow (1980), Stiles & Skutch (1989), Stotz *et al.* (1996), Underwood (1896).

163. Snowy-breasted Hummingbird

Saucerottia edward

French: Ariane d'Edward **German:** Edwardamazilie **Spanish:** Amazilia de Edward
Other common names: White-bellied(ly)/Snowy-bellied Hummingbird (*niveoverter*); Edward's Hummingbird (*edward*)

Taxonomy. *Trochilus edward* DeLattre and Bourcier, 1846, Isthmus of Panama.

Genus usually merged into *Amazilia*. Race *niveoverter* has been considered a distinct species, based mainly on tail coloration and, in this character, lack of intergradation with other races due to strictly allopatric distribution. Individuals with intermediate characters of races *edward* and *margaritarum* have been reported from contact zone in E Panama. Two questionable races were described from the mainland of Panama: the form *croshyi* of Darién (E Panama) was separated by tail coloration from race *margaritarum*, but is indistinguishable from it, as the characters of most individuals of the type series can be accounted for by juvenile plumage; *ludibunda*, described from a single specimen from Pesé in Azuero Peninsula (C Panama), was collected within the eastern range of *niveoverter* and represents an aberrant example of this race. Four subspecies recognized.

Subspecies and Distribution.

S. e. niveoverter (Gould, 1851) - SW Costa Rica to W & C Panama, including Coiba I.

S. e. edward (DeLattre & Bourcier, 1846) - Panama, from Canal Zone to W Darién.

S. e. collata (Wetmore, 1952) - C Panama.

S. e. margaritarum Griscom, 1927 - N Gulf of Panama, in Pearl Is and on Urabá I, Taboga I and Taboguilla I; E Panama to SW Darién.

Doubtfully recorded in Ecuador (Santo Domingo), perhaps race *margaritarum*.



Descriptive notes. 8-11 cm; male 5.0 g, female 4.4 g. Blackish, straight bill, with reddish base to lower mandible. Male has upperparts bronze-green to coppery, especially on back and rump; throat and chest glittering golden green, belly with V-shaped white centre; undertail-coverts rufous, rectrices bronze to coppery, sometimes with purple sheen. Female similar but normally has less intense coloration on upperparts; more whitish on throat and in undertail-coverts; light green tips on outer rectrices. Immature has greyish-brown sides instead of the pure white belly of adults. Race *niveoverter* slightly larger, with tail blue-

ish-black to purplish-black; *collata* has less contrasted back, brownish undertail-coverts; *margaritarum* can be differentiated by paler undertail-coverts and bronze to bronze-green tail.

Habitat. Varies with distribution; in Costa Rica and the western parts of Panama prefers semi-open habitats and savannas with scrub and scattered trees, open woodland, clearings, forest edges, second growth, coffee plantations, flowery thickets, gardens and roadsides. Race *niveoverter* has widest altitudinal tolerance, from near sea-level to 1600 m in Chiriquí, W Panama. Race *collata* is found around El Valle in areas with low, woody-stemmed herbs as well as abandoned fields with low bushes at 500-850 m. Race *margaritarum* shows disjunct range; island populations occur in semi-open to open habitats, abandoned fields, mangrove swamps, and along small streams; mainland population also inhabits rainforest, between sea-level and 700 m.

Food and Feeding. Forages and perches at varying heights, mainly between 3 and 6 m. Usually solitary, but may gather in numbers at flowering trees. Food plants include tree species (*Inga*, *Calliandra*, *Vochysia*, *Quassia*), shrubs (*Palicourea*, *Stachytarpheta*) and a variety of introduced plants. Sometimes feeding territories are defended, even against larger trochilids like *Florisuga mellivora* which can be vigorously pursued. Arthropod diet includes small spiders, flies (Diptera) and Hymenoptera, caught by hawking, often over water, or gleaned from leaves.

Breeding. For western populations, breeding has been recorded between Oct and Jan, with peak Dec-Jan during onset of dry season. Nest is placed on horizontal branch beside vertical stem, or in fork, 1.5-9 m above ground; compact, downy cup of brown fibres, covered on outside with red and green lichens and sometimes green moss. Favourite nesting spots are bushes and smaller trees, often in open areas such as fields or roadsides. Clutch size 2; incubation by female; no information on incubation and fledging periods.

Movements. Western populations at least show local movements. Probably remains in more arid areas during wet season, retreating to the headwaters of rivers during dry season. In Buena Vista Valley, Costa Rica, disappearance of race *niveoverter* correlated with absence of flowering from Feb-Mar to Apr-May; individuals of that race may also migrate along the Atlantic coast as indicated by specimen records from Bocas del Toro, NW Panama.

Status and Conservation. Not globally threatened, CITES II. One of the commonest trochilids in the Canal Zone of Panama; locally common in SW Costa Rica and W Panama in the upper tropical to subtropical zone. Race *collata*, although more restricted in altitude and range than the other races, apparently abundant in open, shrubby habitat; *margaritarum* is relatively common resident in Pearl Is and adjacent islands; within mainland range, becomes uncommon in NW Darién and eastern parts of Panama such as Chucanti and Ultima.

Bibliography. Anon. (1998a), Blake (1958), Carraker (1910), Cory (1918), Deignan (1961), Hartman (1957), Oberholser (1902), Olson (1997), Ridgely & Gwynne (1989), Roubik *et al.* (1985), Skutch (1961a, 1972), Slud (1964), Stiles (1985c), Stiles & Skutch (1989), Stone (1918), Stotz *et al.* (1996), Todd (1942), Wetmore (1946, 1952, 1957a, 1968a), Willis & Eisenmann (1979).

164. Blue-tailed Hummingbird

Saucerottia cyanura

French: Ariane à queue bleue German: Blauschwanzamazilie Spanish: Amazilia Coliazul

Taxonomy. *Amazilia cyanura* Gould, 1859, Realejo, Nicaragua.

Genus usually merged into *Amazilia*. Forms a superspecies with *S. beryllina*; reports of hybridization in a small zone of sympatry in Guatemala and El Salvador seem to be unproven, and may be erroneously based on variable tail coloration of that species. In recent literature only two races have been recognized, with *impatiens* from Costa Rica ignored, perhaps because only two specimens exist; however, morphological characters indicate that it should be considered valid. Races show highly disjunct distribution. Three subspecies recognized.

Subspecies and Distribution.*S. c. guatemalae* Dearborn, 1907 - SE Mexico (SE Chiapas) to S Guatemala.*S. c. cyanura* (Gould, 1859) - S Honduras, E El Salvador and NW Nicaragua.*S. c. impatiens* Bangs, 1906 - NW & C Costa Rica.

Descriptive notes. 9-10 cm; 4.0 g. Male has straight, medium-sized, blackish bill, except for reddish base of lower mandible; crown, nape and back golden to bronze-green; rump with copper to purplish reflections; base of outer secondaries and inner primaries broadly rufous; underparts glittering golden green; uppertail-coverts purple-violet to deep blue, rectrices deep blue, undertail-coverts bluish with grey to rufous edges. Female similar but has reduced wing patch; more greyish areas on throat and belly; edges of undertail-coverts broader greyish. Immature has dull green throat feathers, more greyish to rufous belly and margins of undertail-coverts. Race *guatemalae* shows more copper to purplish back and rump, rufous in wings less extensive; *impatiens* has extended rufous in wings, undertail-coverts broader and darker, edged with rufous.

Habitat. Found in humid and arid forests with pine or oak, second growth, clearings, semi-open to open areas with scrub; also in man-made habitats such as coffee plantations. In Honduras, inhabits arid areas on Pacific slope but also more humid deciduous forest habitats on Caribbean side. Mainly below 1000 m; nominate *cyanura* has altitudinal distribution from near sea-level to 1200 m; *guatemalae* from 150 to 1800 m. Recent localities of race *impatiens* indicate primary forest as original habitat at 500-1000 m.

Food and Feeding. Forages for nectar at various heights; often seen at flowering *Inga* trees. Hawks for insects in the air.

Breeding. No information available.

Movements. Chiefly sedentary, although altitudinal distribution may vary with season.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in North Central American Pacific Slope EBA. Status differs over range. Generally, common in the Pacific lowlands but uncommon on the Caribbean slope of Honduras. Race *guatemalae* locally abundant in SE Mexico and SW Guatemala. Current status of race *impatiens* in Costa Rica unknown; not recorded since 1958, and may be at least close to extinction; the only records, all from this century, amount to two specimens, as well as one possible sighting, although the individuals concerned have often been regarded as northern vagrants; remnant populations, if they still exist, would most likely be found in relatively undisturbed, shrubby woodland habitats within the NW part of the volcanic belt.

Bibliography. Anon. (1998a), Dearborn (1907), Dickey & van Rossem (1938), Friedmann *et al.* (1950), Howell & Webb (1995a), Land (1970), Monroe (1968), Rand & Traylor (1954), Slud (1960, 1964), Stattersfield *et al.* (1998), Stiles (1980), Stiles & Skutch (1989), Stotz *et al.* (1996), Thurber *et al.* (1987), Warren (1966).

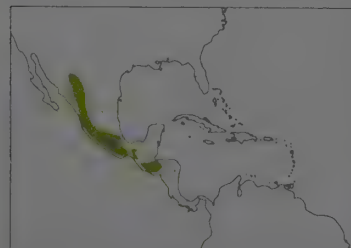
165. Berylline Hummingbird

Saucerottia beryllina

French: Ariane beryl German: Beryllamazilie Spanish: Amazilia Berilina

Taxonomy. *Trochilus beryllinus* Lichtenstein, 1830, Mexico.

Genus usually merged into *Amazilia*. Forms a superspecies with *S. cyanura*; reports of hybridization in a small zone of sympatry in Guatemala and El Salvador seem to be unproven, and may be erroneously based on variable tail coloration of present species. Race *sumichrasti*, long ignored, has proved to represent a well-marked race. Individuals of westernmost subpopulation of nominate race show intergradation towards *viola* in belly coloration. Proposed race *motaguae* from E Guatemala is invalid, as main distinguishing characters can be ascribed to juvenile or female plumage. Five subspecies recognized.

Subspecies and Distribution.*S. b. viola* (W. deW. Miller, 1905) - NW & W Mexico, rarely SW USA.*S. b. beryllina* (Lichtenstein, 1830) - C Mexico.*S. b. lichtensteini* R. T. Moore, 1950 - S Mexico (W Chiapas).*S. b. sumichrasti* (Salvin, 1891) - S Mexico (C & S Chiapas).*S. b. devillei* (Bourcier & Mulsant, 1848) - S Guatemala and El Salvador to C Honduras.

Descriptive notes. 8-10 cm; male 4-4 g, female 4-0 g. Male has straight, medium-sized, blackish bill, except for fleshy-coloured basal half of lower mandible; bronze-green to coppery on head, back and rump; base of primaries and secondaries chestnut; underparts glittering golden green; uppertail-coverts and tail variable, often coppery to rufous. Female similar but has throat and belly paler, more greyish. Immature is similar to female but with less iridescence on throat; belly greyish-cinnamon. Race *viola* has greyish tinge on back and rump, belly fawn to cinnamon, uppertail-coverts and rectrices dark violet-blue; *lichtensteini* is generally lighter green, wing band paler, rectrices silvery-coloured; *sumichrasti* has somewhat purplish gloss to tail. Female with silvery to purple inner rectrices; *devillei* shows stronger bronze to coppery on back and rump, wing band paler, tail purplish to bronzy-chestnut.

Habitat. Inhabits edges of tropical lowland or sub-montane evergreen forest, second growth, clearings, scrub and plantations. Found from foothills to highlands, from 200 m to 2100 m, but chiefly between 400 and 1700 m.

Food and Feeding. Feeds for nectar throughout foliage strata, often congregating with other hummingbird species at flowering trees; catches small insects at spider webs or by hawking. Depending on habitat, feeds on both native and introduced plants, including *Malvaviscus*, *Psittacanthus* and *Calliandra*, also succulents like *Ceiba* and *Lemnaireocereus*. Generalist forager, often occupying feeding territories. On the whole relatively dominant although subdominance was registered where sympatric with *Lampornis amethystinus*.

Breeding. Chiefly Jun-Oct, in Oaxaca with peak in Sept. Nest-sites from low down to 15 m above ground in shrubs and trees such as *Wigandia*, pine and oak, in Arizona also in sycamore (*Platanus*). Nest rather solid, on horizontal branch, made of grass, plant fibres, cotton, and often with a conspicuous streak of grass blades near the bottom that are fixed with cobweb; outside decorated with light-coloured lichens; measures 40-50 mm both in outside diameter and depth, inside depth of c. 15 mm and width of c. 26 mm. Clutch size 2; incubation by female; fledging at about 20 days.

Movements. Sedentary in many parts of the range, except for the extreme north where regular migrant, mainly southward. Occasionally occurs as wanderer or rare breeder in southern Arizona, USA, where records date from mid-Jun to late Sept. Some altitudinal movements observed where birds occur at lower elevations after breeding.

Status and Conservation. Not globally threatened. CITES II. Very local and rare in SW USA, where apparently confined to Huachuca Mts and Chiricahua Mts of Arizona. Few records exist for the E slope of northern Sierra Madre Occidental, with southward distribution at least as far as Barranca del Cobre National Park. Common resident along the Pacific slope and interior highlands from NW Mexico to Guatemala. Uncommon in arid Motagua Valley of NE Guatemala; less common along Atlantic slope from Mexico to C Honduras. Race *lichtensteini* has most restricted range, confined to Cerro Brujo, W Chiapas (Mexico).

Bibliography. Anderson & Monson (1981), Baicich & Harrison (1997), Berlioz (1932b), Binford (1989), Carraker & Meyer de Schauensee (1935), Davis (1953), Des Granges (1979), Des Granges & Grant (1980), Friedmann *et al.* (1950), Hartert & Hartert (1894), Hejl *et al.* (1995), Hernández & Toledo (1980), Howell & Webb (1995a), Johnsgard (1997), Kaufman (1996), Land (1962, 1970), Lasley & Sexton (1992), Lowery & Dalquest (1951), Martínez del Río & Eguiarte (1987), Monroe (1968), Moore (1950b), Ridgway (1911), van Rossem (1945a), Rowley (1962, 1966, 1984), Schaldach (1963), Sheppard (1968), Sitzeman *et al.* (1976), Stager (1954), Stotz *et al.* (1996), Sutton (1952), Tashian (1953), Wagner (1957b), Webster (1959), Weller (1998), Williams (1993), Zimmerman & Harry (1951).

166. Green-bellied Hummingbird

Saucerottia viridigaster

French: Ariane à ventre vert German: Grünbauchamazilie Spanish: Amazilia Colimorada

Taxonomy. *Trochilus viridigaster* Bourcier, 1843, Fusagasuga, Colombia.

Genus usually merged into *Amazilia*. Forms a superspecies with *S. cupreicauda* and *S. tobaci*; normally considered conspecific with former, but morphological differences, in addition to highly disjunct ranges, support their separation as two distinct species. Race *iodura* has generally been overlooked or rejected in recent literature; however, on the basis of morphology, in combination with distribution, it appears to be a valid race; intergradation of the two races may occur south of Táchira depression. Proposed race *melanura* is now regarded as an aberrant form of nominate race. Two subspecies recognized.

Subspecies and Distribution.*S. v. viridigaster* (Bourcier, 1843) - E slope of E Andes of Colombia (S to Sierra Macarena); doubtfully W slope as indicated by the type locality.*S. v. iodura* Reichenbach, 1854 - Andes of Táchira (W Venezuela).

Descriptive notes. 8-9 cm; 4-5 g. Male has straight, medium-sized bill; upper mandible black, lower mostly pinkish with dark tip; head and back golden green; rump and tail-coverts olive green to buff or brownish; uppertail-coverts sometimes with purplish tinge; underparts darker shining green; tail slightly forked, deep blue to violet-blue. Female similar but has throat feathers fringed white; rectrices edged with bronze to brownish. Immature has more brown on rump; belly greyish-brown. Race *iodura* has tail relatively unicoloured coppery to purple in both sexes.

Habitat. Inhabits edges of tropical lowland or sub-montane evergreen forest, second growth, clearings, scrub and plantations. Found from foothills to highlands, from 200 m to 2100 m, but chiefly between 400 and 1700 m.

Food and Feeding. Forages for nectar and small insects in understorey and middle strata. Assembles at flowering trees like *Erythrina*.

Breeding. Poorly known. Birds in breeding condition were found in Oct, Dec, Jan. Clutch size 2; incubation by female; no data exist on duration of incubation or fledging.

Movements. No information available; probably performs some local movements.

Status and Conservation. Not globally threatened. CITES II. Fairly common to uncommon resident of the sub-montane tropical zone of E slope of Andes in Colombia, where occurs southwards at least as far as Macarena Mts. In Venezuela, only recorded in Andes of Táchira, but northern distributional limits require confirmation.

Bibliography. Berlioz (1933a), Blake (1962), Chapman (1917, 1931), Hilty & Brown (1986), Meyer de Schauensee (1949, 1964, 1982), Meyer de Schauensee & Phelps (1978), Nicéforo (1940), Olivares (1963), Olrog (1968), Sánchez (1995), Simon (1921), Stotz *et al.* (1996), Todd (1942).

167. Copper-tailed Hummingbird

Saucerottia cupreicauda

French: Ariane à queue cuivrée German: Kupferschwanzamazilie Spanish: Amazilia Colicobrizza

Taxonomy. *Amazilia cupreicauda* Salvin and Godman, 1884, Mount Roraima, Guyana.

Genus usually merged into *Amazilia*. Forms a superspecies with *S. viridigaster* and *S. tobaci*; normally considered conspecific with former, but morphological differences, especially in coloration

of rump, uppertail-coverts and rectrices, in addition to disjunct ranges, support their separation as two distinct species. Three subspecies recognized.

Subspecies and Distribution.

S. c. cupreicauda (Salvin & Godman, 1884) - highlands and *tepui*s of E Venezuela, Guyana and extreme N Brazil (Roraima).

S. c. duidae Chapman, 1929 - S Venezuela.

S. c. laireti (Phelps, Jr. & Aveledo, 1988) - extreme S Venezuela; possibly N Brazil.



Descriptive notes. 9-10 cm; male 3-9 g, female 3-5 g. Male has straight, medium-sized bill, upper mandible blackish, lower fleshy red with dark tip; crown golden green, nape, back and rump golden green to bronze or coppery, the latter sometimes with purplish reflections; underparts glittering golden green; tail-coverts, base and centre of tail feathers rufous to chestnut; rectrices more or less bicoloured, broadly edged bronze to purple. Female similar but has more prominent white bases to chin feathers; back and tail often less contrasted. Immature has dark grey lower belly to abdomen. Race *duidae* has more coppery lower back and rump,

rectrices bronze to purplish, basally lacking rufous; *laireti* is slightly darker green, with uppertail-coverts and rectrices uniformly golden bronze to copper.

Habitat. Mainly found along forest edges, in clearings and scrub. Ranges from foothills to highlands, inhabiting slopes as well as tops of *tepui*s. Nominant race mostly found between 500 and 1300 m, rarely below though once recorded at 85 m in Kanuku Mts, Guyana. Race *duidae* is a bird of primary forest edges, with an upper altitudinal limit of c. 1400 m. By contrast, *laireti* prefers open to semi-open shrubland with vegetation dominated by bromeliads and terrestrial orchids, mainly in the subtropical zone between 750 and 1850 m.

Food and Feeding. Poorly known; diet includes nectar as well as small insects and spiders. Race *laireti* recorded feeding on epiphytes.

Breeding. Season not well known but at least Jan-May. One nest, found in Feb in Kanuku Mts, contained two nestlings: it was situated in a small tree, 3 m above ground, placed at the end of a branch and fixed between twigs with cobweb; outside was covered with moss, lichens, cobweb, inside lined with thick, tawny plant down. Clutch size 2; incubation by female; no data exist on incubation and fledging periods.

Movements. Chiefly sedentary; seasonal altitudinal movements may occur.

Status and Conservation. Not globally threatened. CITES II. Fairly common to uncommon, but different populations isolated. Distribution of race *cupreicauda* apparently concentrated in La Gran Sabana region and Mt Roraima National Park, along the Venezuelan-Guyanese border. Race *duidae* most common in Duida-Marahuaca National Park. Southernmost race *laireti* has been recorded from only two localities but seems to be locally abundant in Serranía de la Neblina National Park. Presumably, current extent of distribution of the southern races exceeds known ranges due to collecting gaps in the SE highlands of Venezuela and adjacent areas such as Roraima, Brazil.

Bibliography. Barrowclough *et al.* (1995), Berlioz (1933a), Chapman (1929, 1931), Chubb (1916), Cory (1918), Forrester (1993), Grantsau (1988), Haverschmidt & Mees (1994), Mayr & Phelps (1967), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Novas (1965), Phelps (1972), Phelps & Aveledo (1988), Ruschi (1981-1982, 1986), Sánchez (1995), Sick (1993, 1997), Snow & Snow (1974), Snyder (1966), Willard *et al.* (1991).

168. Copper-rumped Hummingbird

Saucerottia tobaci

French: Ariane de Félicie **German:** Kupferbüzelamazilie **Spanish:** Amazilia de Tobago
Other common names: Common Emerald

Taxonomy. *Trochilus Tobaci* J. F. Gmelin, 1788, Tobago.

Genus usually merged into *Amazilia*. Forms a superspecies with *S. viridigaster* and *S. cupreicauda*. Proposed race *apurensis* most probably falls within individual variation of race *feliciae*. A specimen said to have been taken on Grenada, and described as "*S. wellsii*", has alternatively been

treated as a vagrant of nominate race; however, its true origin appears dubious. Seven subspecies recognized.

Subspecies and Distribution.

S. t. tobaci (J. F. Gmelin, 1788) - Tobago.

S. t. erythronotos (Lesson, 1829) - Trinidad.

S. t. aliciae (Richmond, 1895) - I Margarita, Venezuela.

S. t. monticola Todd, 1913 - NW Venezuela.

S. t. feliciae (Lesson, 1840) - NC Venezuela.

S. t. caudata (Zimmer & Phelps, 1949) - NE Venezuela.

S. t. caurensis Berlepsch & Hartert, 1902 - E & SE Venezuela.



Descriptive notes. 9-11 cm; male 4-6 g, female 4-2 g. Male has straight, medium-sized, blackish bill, except for pinkish base of lower mandible; upperparts bronze-green; underparts glittering dark golden green; uppertail-coverts purple-red; undertail-coverts reddish-brown; rectrices purplish-black. Female similar but coloration of back normally less intense; whitish on chin and upper throat. Immature has throat and belly partially greyish-brown. Other races differ morphometrically from nominate, which is by far the largest; *erythronotos* slightly darker below, with centres of uppertail-coverts dark purplish; *monticola* is generally darker,

less contrasted, with rectrices steel-blue to violet-blue, undertail-coverts reddish-brown; *feliciae* has back more glittering golden to bronze-green, tail bluish-black, undertail-coverts reddish-brown; *caudata* has tail dark blue, *aliciae* has more copper in upperparts and tail blue-black, both with undertail-coverts cinnamon-rufous; *caurensis* is greyer on rump and uppertail-coverts, tail less bifurcated, dark purplish, undertail-coverts bluish black.

Habitat. Inhabits nearly all types of forest, including gallery forest, cloudforest and rainforest, and also second growth and clearings; island races *erythronotos* and *tobaci* also occur in open country with savanna-like vegetation, plantations and gardens. Ranges mainly between sea-level and 1000 m; some mainland races like *monticola* and *feliciae* reach 1500-2000 m. In contrast to other island races, *aliciae* of Margarita I seems to prefer mountainous areas.

Food and Feeding. Feeds mainly on nectar of a great variety of plants; more than 40 species of trees, particularly *Erythrina* and *Calliandra*, shrubs (*Palicourea*), vines (*Gurania*), herbs (*Pachystachys*) and various introduced plants (*Hibiscus*, *Russelia*) were recorded for Trinidad and Tobago. Forages for insects in vegetation, or hawks over fallen fruits for small flies. Extremely territorial; dominates other hummingbirds, even larger species. Attacks any intruders within the feeding area, either directly or sometimes in pendulum-like flight if intruder perched. Insects are caught in the air by hawking.

Breeding. Poorly known in mainland races. On Trinidad, breeding recorded from all months except Sept-Oct, with main season Jan-Mar. On Tobago, nesting noted Nov-Jun. Saddle-type nest, usually placed in fork or on branch of small tree or bush, 1-3 m above ground, sometimes up to 6 m; nests occasionally found on wires, clothes-lines(!), etc. Cup is made of silky plant down, sometimes with coconut fibres or scales of fern fronds, decorated with pieces of lichen and cobweb. Clutch size 2; incubation 16-19 days, by female; fledging period 19-23 days. 2-3 broods per season, at intervals of 1 week to 1 month.

Movements. Insular races generally sedentary, though claimed record from Grenada could refer to a vagrant; some birds of mainland races perform local movements.

Status and Conservation. Not globally threatened. CITES II. Common to very common on the islands of Trinidad and Tobago, where frequently found even in urban areas. Race *feliciae* represents the commonest of the mainland races, occurring in city parks in Caracas, etc. Race *caudata* also common, frequently occurring in gardens and other man-made habitats. Distribution of other Venezuelan races, *caurensis* for example, appears more scattered, possibly due in part to a lack of collecting sites.

Bibliography. Allen (1961), Anon. (1985a), Barrowclough *et al.* (1997), Belcher & Smooker (1936), Berlioz (1933a), Clark, A.H. (1902), Dinsmore & French (1969), Feinsinger (1980), Feinsinger & Swann (1982), French (1991), Friedmann (1948), Friedmann & Smith (1950), Gilliard (1941), Hayes & Samad (1998), Herklots (1961), Jouanin (1946), Junge & Mees (1961), Meyer de Schauensee & Phelps (1978), Muir & Butler (1925a), Rieckels (1968), Sánchez (1995), Stotz *et al.* (1996), Thomas (1993), Todd (1942), Wetmore (1939), Zimmer & Phelps (1949).

inches 2
cm 5



Genus *MICROCHERA* Gould, 1858

169. Snowcap

Microchera albocoronata

French: Colibri à coiffe blanche **German:** Schneekappenkolibri **Spanish:** Colibri Coroniblanco
Other common names: White-crowned Hummingbird

Taxonomy. *Mellisuga albo-coronata* Lawrence, 1855, Belén, Veraguas, Panama.

Two subspecies recognized.

Subspecies and Distribution.

M. a. parvirostris (Lawrence, 1865) - Caribbean slope of S Honduras, Nicaragua, Costa Rica and probably extreme W Panama.

M. a. albocoronata (Lawrence, 1855) - both slopes of WC Panama.



Descriptive notes. 6-6.5 cm; male 2.5 g, female 2-6 g. Bill and feet black. Male has entire crown glistening white, throat glossed green, rest of head and underparts purplish-black; remainder of upperparts metallic reddish-purple, passing to metallic bronze on central rectrices, lateral rectrices with basal half or more white, rather sharply set off from black terminal band. Female metallic green above, greyish-white below, uppertail-coverts and central rectrices bronze; lateral rectrices with basal half or more white, rather sharply set off from black subterminal band. Immature of both sexes resembles adult female but greyer below, with greyish-buff to rusty feather fringes over much of upperparts; lower upperparts of young male more bronzy, less purplish; purple feathers on underparts of young male first appear along mid-line, producing striking dark medial stripe. In race *parvirostris*, male is reddish-purple above and below, generally brighter than nominate; throat dusky brown, underparts bright reddish-purple; in both sexes the lateral rectrices are extensively clouded with dusky grey proximal to the dark band.

Habitat. Wet forest, forest edges, adjacent semi-open and second growth in foothills and lowlands; male more in subcanopy and canopy, coming down lower along edges and in second growth; female frequents understorey and middle strata in forest, often higher in semi-open habitat. In Costa Rica, breeds at 300-800 m, rarely 1000 m; after breeding descends to lowlands; occurs at 600-1650 m in Panama.

Food and Feeding. Visits mostly small flowers of trees (*Warscewiczia*, *Sickingia*, *Inga*, *Pithecellobium*), shrubs (*Sabicea*, *Besleria*, *Hamelia*, *Cephaelis*, *Psychotria*), vines (*Gurania*) and epiphytes (*Columnea*, *Norantea*, *Cavendishia*) in forest, often frequenting hedges of *Stachytarpheta* in adjacent gardens. Male may defend feeding territories against other conspecifics but is displaced by most other species. Gleans insects and spiders from foliage; male often sallies for flies and gnats.

Breeding. Dry to early wet seasons (Jan-May) in Costa Rica. During breeding season male sings a soft, sputtering warble from exposed twigs 4-8 m up at forest edge, usually in small leks of 3-6. Nest a tiny cup of treefern scales, plant down and cobweb, lightly decorated with green moss and with a few bits of lichen around the rim, 1-5.3 m up on lower twig of tree, or vine hanging from tree. No further information.

Movements. Descends to lowlands (regularly to 50-100 m, occasionally to sea-level) following breeding.

Status and Conservation. Not globally threatened. CITES II. While deforestation is severe in many parts of range in Costa Rica, species remains locally common in others, such as the lower part of Braulio Carrillo National Park and Rara Avis Reserve, although its preferred foothill elevations are below the limits of most protected areas.

Bibliography. Anon. (1998a), Carriker (1910), Fogden (1993), Howell, S.N.G. & Webb (1995a), Howell, T.R. (1957), Marin & Schmitt (1991), Monroe (1968), Ridgely & Gwynne (1989), Ridgway (1911), Slud (1964), Stiles (1980, 1985b, 1985c), Stiles & Clark (1989), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968a).

Genus *ANTHOCEPHALA* Cabanis & Heine, 1860

170. Blossomcrown

Anthocephala floriceps

French: Colibri à tête rose **German:** Blaustrirnkolibri **Spanish:** Colibrí Florido

Taxonomy. *Trochilus* (—?) *floriceps* Gould, 1854, Sierra de Santa Marta, Colombia.

Systematic relationships uncertain; perhaps closely related to *Microchera*; sometimes alternatively considered close to *Adelomyia*, and possibly even congeneric. Two subspecies recognized.

Subspecies and Distribution.

A. f. floriceps (Gould, 1854) - Santa Marta Mts (NE Colombia).

A. f. berlepschi Salvin, 1893 - Magdalena Valley, on E slope of C Andes (C Colombia).

Descriptive notes. c. 8-4 cm. Male has straight, black bill; forecrown buffy white, hindcrown rufous chestnut, rest of upperparts shining green, postocular spot white; underparts greyish-buff, tail squared, bronzy-green, tipped pale buffy, black subterminal bar, lacking on central pair of rectrices. Female similar to male, crown brownish. Immature resembles adult female. Race *berlepschi* differs in having largely white tips to tail.

Habitat. Humid forest and older second growth. Generally found at 1200-2300 m; in Santa Marta, normally at 600-1700 m, but one nesting record at 2400 m.



Food and Feeding. No specific food plants have been recorded, except for flowering banana. Usually forages at low levels in understorey.

Breeding. Birds in breeding condition Sept-Oct, Santa Marta. No further information available.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Currently considered Near-threatened. Restricted-range species: present in Santa Marta Mountains EBA and Colombian Inter-Andean Slopes EBA. Generally rare, but locally abundant in parts of Santa Marta. In conjunction with small range, species may be

vulnerable to habitat destruction; not known to accept man-made habitats.

Bibliography. Fjeldså & Krabbe (1990), Hilty (1985), Hilty & Brown (1986), Meyer de Schauensee (1982), Olrog (1968), Renjifo *et al.* (1997), Ridgely & Gaulin (1980), Salaman & Mazariegos (1998a), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Todd & Carriker (1922).

Genus *CHALYBURA* Reichenbach, 1854

171. White-vented Plumeleteer

Chalybura buffonii

French: Colibri de Buffon **German:** Blauschwanz-Buffonkolibri **Spanish:** Colibrí de Buffon
Other common names: Buffon's Hummingbird; Blue-bellied Plumeleteer (*caeruleogaster*)

Taxonomy. *Trochilus Buffonii* Lesson, 1832, Brazil; error = Bogotá region, Colombia.

Type specimen has sometimes been ascribed to populations from Panama and W Colombia, with consequent reshuffling of subspecific nomenclature; under that arrangement, birds currently listed as nominate become race *interior*, whereas those of current race *micans* become nominate. Another variation occasionally adopted, under present arrangement with type locality of Bogotá region, involves population around L Maracaibo basin being split as a separate race, for which name *interior* is likewise available; however, these differences are slight, and subspecific separation of Maracaibo birds unjustified. In past, race *caeruleogaster* often considered a separate species. Race *intermedia* of *C. urochrysis*, from SW Ecuador, sometimes ascribed to present species, but its largely pinkish mandible supports treatment in that species; nevertheless, it might be better considered a separate species; more study required. Four subspecies recognized.

Subspecies and Distribution.

C. b. micans Bangs & Barbour, 1922 - C & E Panama and W Colombia (Pacific slope, Cauca Valley and head of Magdalena Valley).

C. b. buffonii (Lesson, 1832) - C Colombia (upper and middle Magdalena Valley) to S & W parts of L Maracaibo basin and adjacent slopes in extreme NE Colombia and NW Venezuela.

C. b. aeneicauda Lawrence, 1865 - N Colombia (lower Magdalena Valley and Santa Marta region) to W & NC Venezuela (along S slope of Andes and on coastal slope).

C. b. caeruleogaster (Gould, 1847) - N & C Colombia (E slope of E Andes).



Descriptive notes. 10-5-12 cm; male 6-9-7.3 g, female 5-9-6.2 g. Bill always completely black, feet black. Male of nominate dark metallic green above, crown and hindneck more bronzy, uppertail-coverts more coppery-bronze; below bright metallic green, bluish on upper breast, lower belly whitish, undertail-coverts elongated, fluffy, white; tail blue-black, the central rectrices glossed bronzy. Female is grey below, rather heavily speckled with green laterally and sometimes across chest, lateral rectrices tipped dull grey. Immature male duller green below; both sexes with some buffy fringes on crown, nape and rump feathers. Race

micans larger, central rectrices deeper blue, female clearer grey below; male of *aeneicauda* often more golden green below, central rectrices bright bronze-green to copper-bronze. Female pale grey below with sparse green flecking; race *caeruleogaster* larger, male with throat and belly bluish-green, breast blue, female clear grey below, immature male with little or no blue below.

Habitat. Dry, moist and wet forests, forest edges, semi-open and second growth; in wetter areas where sympatric with *C. urochrysis* prefers more open, scrubby places rather than forest; only *caeruleogaster* and to a lesser extent *buffonii* occur regularly inside wet forest. Found from sea-level locally to 2000 m.

Food and Feeding. Takes nectar from flowers of a variety of trees (*Inga*, *Calliandra*, *Trichanthera*, *Erythrina*), shrubs (*Aphelandra*, *Malvaviscus*, *Hibiscus*, *Hamelia*, *Palicourea*) and large herbs (*Heliconia*); very aggressive and dominant at flowers, supplanting other hummingbirds in aggregations at flowering trees, male often territorial at rich patches of flowers; may pierce flowers with long corollas. Frequently flycatches, sallies from perch or during prolonged bouts of hovering and darting, usually in open or along edges; also sometimes gleans arthropods from foliage or spiders' webs.

Breeding. Mar-Jul or Aug (*buffonii*, Magdalena Valley); Jun-Nov (*caeruleogaster*). Nest is a neat cup of plant down and cobweb, decorated with pieces of lichen and bits of moss; one nest of *caeruleogaster* 2.5 m above ground in guava tree in garden adjoining forest. No further information.

Movements. No information available.

Status and Conservation. Not globally threatened. CITES II. Uncommon to fairly common in most areas, and seems able to tolerate considerable disturbance, taking advantage of forest clearance in wetter areas over most of range. Only race *caeruleogaster* seems likely to have declined, due to deforestation of lower Andean slopes and adjacent lowlands over much of range, though it

remains at least locally common in some areas. In Venezuela, species occurs in several protected areas such as Cueva del Guácharo and Henri Pittier National Parks.

Bibliography. Anon. (1998a), Hilty & Brown (1986), Meyer de Schauensee & Phelps (1978), Olrog (1968), Parker *et al.* (1995), Phelps & Phelps (1958), Ridgely & Gwynne (1989), Stotz *et al.* (1996), Todd (1942), Wetmore (1968a), Wiedenfeld *et al.* (1985), Willis & Eisenmann (1979).

172. Bronze-tailed Plumeleteer

Chalybura urochrysis

French: Colibri à queue bronzée

Spanish: Colibrí Pátrirjo

German: Bronzeschwanz-Buffonkolibri

Other common names: Red-footed Plumeleteer; Black-vented/Dusky Plumeleteer (*melanorrhoea*); Ecuadorian Plumeleteer (*intermedia*)

Taxonomy. *Hypoprottila urochrysis* Gould, 1861, western Colombia.

Race *melanorrhoea* long considered a separate species, but intergrades with *isaurae* along border of Costa Rica with Panama. Geographically isolated race *intermedia* often placed in *C. buffoni*, but its largely pinkish mandible supports treatment in present species; nevertheless, it might be better considered a separate species; more study required. Proposed race *incognita* probably best treated as a synonym of *isaurae*. Four subspecies recognized.

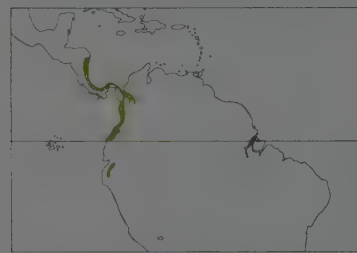
Subspecies and Distribution.

C. u. melanorrhoea Salvin, 1865 - Caribbean slope of Nicaragua and Costa Rica.

C. u. isaurae (Gould, 1861) - Caribbean slope of Panama to extreme NW Colombia; locally on Pacific slope in W & C Panama, and extensively in E Panama.

C. u. urochrysis (Gould, 1861) - extreme SE Panama, NC & W Colombia, and extreme NW Ecuador.

C. u. intermedia E. Hartert & C. Hartert, 1894 - subtropical zone of SW Ecuador.



Descriptive notes. 10.5-12 cm; male 7-1 g, female 6-1 g. Conspicuous red or pink feet (no definite information for *intermedia*); bill black with basal half or more of mandible pinkish. Male of nominate metallic green above, glittering green below with tail bronze-green, undertail-coverts fluffy, white, elongated. Female is grey below, flecked with green laterally, the undertail-coverts greyish-white, the lateral rectrices tipped grey. Immature male typically duller below than adults; young of both sexes with buffy to cinnamon fringes on crown, nape and rump feathers. Male *melanorrhoea* glittering dark green below, belly

dusky bronze, undertail-coverts sooty blackish, less elongated; dark bronzy-green above, uppertail-coverts purplish-bronze, tail purplish-black; female darker grey below, more heavily flecked green than in other races, tail as male but lateral rectrices grey-tipped. In race *isaurae*, male is glittering bluish-green below with blue throat and breast, tail brighter bronze; female paler, more immaculate grey below. Birds from near Colombia-Panama border ("*incognita*") intermediate, most like nominate; male of *intermedia* has breast greenish-blue, belly grey, tail dark blue.

Habitat. Understorey and middle strata of humid forest, forest borders, adjacent tall second growth and semi-open habitats (cacao plantations, shaded gardens, etc.); avoids open areas. Occurs from sea-level to 700 m in Costa Rica, 900 m in Colombia.

Food and Feeding. Both sexes visit mainly flowers of large herbs (*Renalemia*, *Costus* and especially *Heliconia*) and shrubs (*Cephaelis*, *Malvaviscus*, *Acanthaceae*), as well as epiphytes of forest middle strata and subcanopy (*Ericaceae*, *Gesneriaceae*, bromeliads), and trees of the understorey or low along borders and gaps (*Inga*, *Symphonia*, *Hamelia*). Very aggressive and dominant at flowers, male in particular often defending territories at the richest clumps, especially of *Heliconia*. Flycatches frequently, mostly in sallies from perch in upper understorey; also makes sallies to glean arthropods from foliage, and less often hovers to glean (especially female); arthropods taken include mostly flies and tiny wasps with small numbers of ants, homopterans, spiders and other taxa.

Breeding. In Costa Rica, Dec or (more often) Feb-May; Feb-Apr in W Colombia. Breeding male often defends flower-centred territories which are visited by females. Nest a deep, compact cup of light-coloured plant down and fibres, and spiders' webs, heavily decorated on outside with green moss and a few bits of lichen. 0.5-1.5 m above ground in shrub near stream or trail in forest understorey (*melanorrhoea*). No further information.

Movements. In *melanorrhoea*, mainly local movements in response to seasonal shifts in flowering; no data for other races.

Status and Conservation. Not globally threatened, CITES II. In some parts of range such as Costa Rica and N Colombia, species has suffered considerable loss of forest habitat, but it remains locally common at some sites. Has been recorded at Finca La Selva and Cahuita National Park (Costa Rica) and at El Placer (Ecuador). Status of race *intermedia* requires investigation.

Bibliography. Best *et al.* (1997), Butler (1979), Chapman (1917, 1926), Eisenmann & Howell (1962), Haffer (1967), Hilty & Brown (1986), Howell, S.N.G. & Webb (1995a), Howell, T.R. (1957), Parker *et al.* (1982), Ridgely & Gwynne (1989), Ridgway (1911), Slud (1964), Stiles (1975, 1980, 1995a, 1995b), Stiles & Skutch (1989), Stotz *et al.* (1996), Weathers & Stiles (1989), Wetmore (1968a), Wiedenfeld *et al.* (1985), Williams & Tobias (1994).

Genus LAMPORNIS Swainson, 1827

173. Blue-throated Hummingbird

Lampornis clemenciae

French: Colibri à gorge bleue

German: Blaukehlhympe

Spanish: Colibrí Gorgiazul

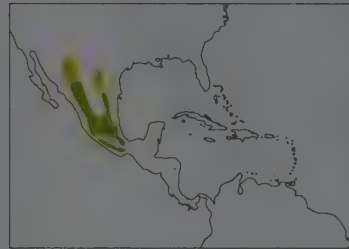
Taxonomy. *Ornismya Clemenciae* Lesson, 1829, Mexico.

Probably a sister-species of *L. amethystinus*. Hybridizes with both *Calypte anna* and *C. costae*. Differences between races are weak and require more study. Two subspecies currently recognized.

Subspecies and Distribution.

L. c. bessophilus (Oberholser, 1918) - SW USA (SE Arizona, S New Mexico) to NW Mexico (E Sonora, W Chihuahua).

L. c. clemenciae (Lesson, 1829) - S USA (SW Texas) and NE, C & S Mexico (Sierra Madre Oriental and central plateau S to Oaxaca).



Descriptive notes. c. 13 cm; male c. 8 g, female c. 6-5 g. Male has medium sized, slightly decurved black bill; crown green, postocular stripe white and dusky grey auriculars; back greyish-green; gorget is iridescent blue often bordered by a white "moustache"; underparts dusky grey; tail rounded, blue-black with broad white tips to outer rectrices. Female similar to male except throat is dusky grey. Immature resembles adult female, immature male with some iridescent blue feathers on throat. Race *bessophilus* has shorter bill, plumage above generally duller, below generally paler.

Habitat. In USA and N Mexico found primarily in riparian canyons at altitude of between 1500 and 2500 m. Associated primarily with pine, oak, cypress, sycamore and maple. Will stray from riparian zones to more arid slopes and disturbed areas to feed. In other parts of Mexico has wider altitudinal range (1500-3500 m) and perhaps weaker association with riparian habitats during breeding season. Descends as low as 500 m during winter when food at higher altitude is scarce.

Food and Feeding. Floral nectar from several plant species, including *Lobelia*, *Nicotinia*, *Penstemon* and *Salvia*; also small arthropods, such as Hemiptera, small beetles, flies and wasps. Exclusive access to food is maintained by intense territorial behaviour. Its large size allows easy dominance over other hummingbird species.

Breeding. In USA mainly between May and Jul. In Mexico the breeding period is more variable, possibly corresponding to specific flowering periods. Nests are constructed in places where completely covered from above, including under the eaves of houses. Nest is a cup lined with soft downy plant materials, exterior is covered with lichen, moss, or bark glued in place with spiderweb. Clutch size 2; incubation 15-18 days by female; fledging at 24-29 days. At least one documented case of 3 broods during one breeding season.

Movements. Birds in S Mexico are resident although some engage in altitudinal migration during winter. In N & C Mexico birds migrate north to breeding grounds, arriving in Mar and Apr. Departure on autumn migration is more variable, occurring between Aug and Oct.

Status and Conservation. Not globally threatened, CITES II. In USA, artificial feeders maintain unusually large populations that exceed available natural food resources. Species is susceptible to natural or unnatural disturbances like forest fires because habitat is often restricted to the higher elevations of isolated mountain ranges. Habitat destruction could prove to be a significant concern in the future throughout range.

Bibliography. Baich & Harrison (1997), Baldrige *et al.* (1983), Bené (1947), Bent (1940), Binford (1989), Cottam & Knappen (1939), DeGraaf & Rappole (1995), Des Granges & Grant (1980), Friedmann *et al.* (1950), Hejl *et al.* (1995), Howell & Webb (1995a), Johnson (1997), Kaufman (1996), Kuban & Neill (1978, 1980), Lasiewski & Lasiewski (1967), des Lauriers (1994), Lyon (1976), Lyon & Chadek (1971), Lyon *et al.* (1977), Marshall (1957), Mayr & Short (1970), Miller (1955), Nosedal (1981), Phillips *et al.* (1964), Pimm (1978), Pimm *et al.* (1985), Powers & Conley (1994), Price *et al.* (1995), Rappole *et al.* (1995), Ridgway (1911), Rising (1965), Rowley (1984), Rutgers & Norris (1972), Schuchmann (1985b), Small (1994), Spofford (1980), Stotz *et al.* (1996), Urban (1959), Wagner (1951, 1952, 1957b).

174. Amethyst-throated Hummingbird

Lampornis amethystinus

French: Colibri à gorge améthyste **German:** Rotkehlhympe **Spanish:** Colibrí Amatistino
Other common names: Cazique Hummingbird; Margaret's/Violet-throated Hummingbird (*margaritae*)

Taxonomy. *Lampornis amethystinus* Swainson, 1827, Temascaltepec and Real del Monte, Mexico. Taxonomy somewhat confused, and precise distributions of races not well known. Probably a sister-species of *L. clemenciae*. Race *margaritae* (including *salvini* and *nobilis*) sometimes suggested as possible separate species. Proposed race *brevirostris* doubtfully distinct from *margaritae*. Race *circumventris* known only from type locality. Five subspecies recognized.

Subspecies and Distribution.

L. a. amethystinus Swainson, 1827 - W, C & E Mexico (S Nayarit, S Nuevo León and S Tamaulipas to Veracruz and E Oaxaca).

L. a. margaritae (Salvin & Godman, 1889) - SW Mexico (Michoacan, Guerrero, W Oaxaca).

L. a. circumventris (Phillips, 1966) - S Mexico (San Gabriel Mixtepec, in SW Oaxaca).

L. a. salvini (Ridgway, 1908) - highlands of S Mexico (Chiapas), Guatemala and El Salvador.

L. a. nobilis Griscom, 1932 - highlands of Honduras.



Descriptive notes. 11.5-12.5 cm; male 5-7.8 g, female 5-5.8 g. Male has slightly decurved black bill; crown dark green, auriculars dusky grey, postocular stripe white, rest of upperparts grey, rump bronzy, uppertail-coverts blackish; underparts dusky grey washed green, gorget iridescent rosy pink, undertail-coverts fringed pale buff; tail slightly forked, bluish-black, outer rectrices tipped grey. Female similar, throat pale dusky cinnamon. Immature resembles adult female, immature male with some pink feathers on throat. Male of race *circumventris* differs in pinkish-purple throat and generally paler coloration of underparts;

margaritae is generally darker in plumage coloration, throat violet-purple but extremely variable; *salvini* is darker and smaller, throat reddish; *nobilis* is similar to previous race but smaller and darker, throat reddish.

Habitat. Edges and interior of humid evergreen and pine-oak forest, at 900-3000 m.

Food and Feeding. Feeds on nectar of flowering *Centropogon affinis*, *Fuchsia minutiflora*, *Penstemon kunthii*, *Rigidella orthantha*, *Salvia caciaefolia*, *S. cinnaberrina*, *S. nervata* and *Satureja*. Feeds by trap-lining. Insects are caught in the air by hawking.

Breeding. Oct-Dec, May-Jul. Nest is cup-shaped, made out of moss, decorated with lichens, and attached to pendulous twigs in bushes or young trees 1.2-2.4 m above ground. Clutch size 2, incubation by female. No further information.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Generally common, but parts of habitat are under threat of deforestation; not known to accept man-made habitats. Regularly recorded at El Triunfo Biological Reserve and Lagos de Montebello (S Chiapas), Volcán de Fuego (Jalisco), Sierra de Atoyac (Guerrero), Cerro San Felipe (Oaxaca) and near San Cristóbal de las Casas (C Chiapas).

Bibliography. Anon. (1998a), Binford (1989), Contreras-Balderas (1997), Des Granges (1979), Des Granges & Grant (1980), Friedmann *et al.* (1950), Griscom (1932c), Hernández-Baños *et al.* (1995), Howell & Webb (1995a), Johnsgard (1997), Land (1970), Lara & Ornelas (1998), Lyon (1976), Monroe (1968), Phillips (1966), Ridgway (1911), Rowley (1966), Skutch (1967), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Wagner (1946a, 1957b), Wetmore (1941).

175. Green-throated Mountain-gem

Lampornis viridipallens

French: Colibri vert-d'eau **German:** Grünkehlnymphe **Spanish:** Colibrí Gorgiescamoso

Taxonomy. *T[rochilus] viridi-pallens* Bourcier and Mulsant, 1846, Cobán, Vera Paz, Guatemala. Forms a superspecies with *L. sybillae*, with which has been considered conspecific. Races *ovandensis* and *nubivagus* doubtfully valid, as differences weak; perhaps best treated as synonyms of nominate. Proposed race *connectens*, known by single specimen from N El Salvador, falls within normal range of variation of nominate. Four subspecies currently recognized.

Subspecies and Distribution.

L. v. amadoni Rowley, 1968 - Cerro Baul in Oaxaca (S Mexico); known only from type locality.
L. v. ovandensis (Brodkorb, 1939) - highlands of S Mexico (Chiapas) and NW Guatemala.
L. v. viridipallens (Bourcier & Mulsant, 1846) - highlands of Guatemala, extreme N El Salvador and W Honduras.
L. v. nubivagus Dickey & van Rossem, 1929 - El Salvador.



Descriptive notes. 11-12 cm; c. 5.4 g. Male has straight black bill; upperparts green, bronzy on rump, postocular stripe white, auriculars darkish, uppertail-coverts bluish-black; throat white with bluish-green iridescent discs, breast white, rest of underparts greyish, mottled green on sides and flanks, undertail-coverts dusky grey; tail slightly forked, central rectrices black, remainder pale grey. Female similar to male, upperparts generally emerald green, throat white. Immature resembles adult female, but throat pale buffy. Race *amadoni* is darker, less bronzy on rump, central rectrices black; *ovandensis* differs in having less green areas

on sides of breast and flanks; in *nubivagus* upperparts are dark green, rump intense bronze.
Habitat. Edge and interior of humid evergreen and pine-oak forest, at 900-2700 m. Forages from low to higher strata.

Food and Feeding. No specific food plants have been recorded. Presumably feeds on nectar of similar flowering plants as *L. amethystinus*, like Campanulaceae, Onagraceae, or *Salvia*. Insects are caught in the air by hawking.

Breeding. Mar-Apr, Jun-Jul. No further data available.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in North Central American Highlands EBA. Generally common, though parts of habitat are under threat of deforestation; not known to tolerate man-made habitats. Regularly recorded at El Triunfo Biological Reserve and Lagos de Montebello (S Chiapas).

Bibliography. Anon. (1998a), Berlioz (1938), Binford (1989), Dickey & van Rossem (1929), Edwards & Lea (1955), Friedmann *et al.* (1950), González-García (1993), Hernández-Baños *et al.* (1995), Howell & Webb (1995a), Land (1970), Monroe (1963, 1968), Paynter (1957), Rowley (1966, 1968), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Wagner (1957b).

176. Green-breasted Mountain-gem

Lampornis sybillae

French: Colibrí de Sybil **German:** Grünbrustnymphe **Spanish:** Colibrí de Sibila

Taxonomy. *Delatratia sybillae* Salvin and Godman, 1892, Matagalpa, Nicaragua. Forms a superspecies with *L. viridipallens*, with which has been considered conspecific. Monotypic.
Distribution. Highlands of E Honduras and NC Nicaragua.



Descriptive notes. 11-12 cm. Male has straight black bill, whitish postocular stripe and dark auriculars, upperparts green, rump bronzy; glittering green gorget with extensive green underparts; tail fairly long and broad, squared to slightly forked, outer rectrices contrasting white. Female similar to male, gorget not clearly defined, throat washed buff. Immature male resembles female but throat whitish, only faintly washed buff.

Habitat. Highland humid evergreen forest, forest edges, oak woodland, brush and thickets, at 1400-2200 m.

Food and Feeding. No information available.

Presumably feeds on similar flowers to *L. viridipallens*.

Breeding. No information available.

Movements. No reliable information available. Presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in North Central American Highlands EBA. Common to fairly common throughout much of its limited range. Species very poorly known; extensive research required.

Bibliography. Anon. (1998a), Berlioz (1938), Hernández-Baños *et al.* (1995), Howell & Webb (1995a), Monroe (1963, 1968), Stattersfield *et al.* (1998), Stotz *et al.* (1996).



PLATE 60

177. White-bellied Mountain-gem

Lampornis hemileucus

French: Colibri à gorge lilas German: Veilchenkehlnympe Spanish: Colibrí Gorgivioleta

Taxonomy. *Oreopyra hemileuca* Salvin, 1865, Turrialba, Costa Rica. Monotypic.

Distribution. Highlands on Caribbean slope from NC Costa Rica to W Panama.



Descriptive notes. 10-11 cm; male 6-2 g, female 5-1 g. Bill black, feet dark flesh-coloured. Adult male has crown and face glittering green, postocular stripe white, rest of upperparts bronzy-green, uppertail-coverts and tail bronzy, lateral rectrices with a dusky grey subterminal band; centre of throat blue-violet, remainder of underparts white, speckled laterally with green. Female similar but crown less glittering green and lacks blue-violet on throat; lateral rectrices tipped grey. Immature male lacks glittering green on head, violet of adult throat replaced by dull bronze; young of both sexes with rusty fringes on feathers of head, back, rump and sides.

Habitat. Canopy and edge of cool, very wet subtropical forest, descending to shrub level along borders, gaps and areas of open understorey; infrequent in adjacent second growth and semi-open vegetation. Breeds at 700-1400 m in Costa Rica.

Food and Feeding. Visits flowers of trees (*Calliandra*, *Clusia*, *Inga*) and shrubs (*Acanthaceae*, *Besleria*, *Cephaelis*), but especially fond of those of epiphytes (*Ericaceae*, *Columnnea*). Notably aggressive when feeding, dominating other species at flowering trees; male often defends rich clumps of flowers of large epiphytes (*Cavendishia*, *Thibaudia*). Frequently flycatches by sallying from perch in canopy or along edge, less often (mostly females) glean arthropods from foliage.

Breeding. Aug or Sept-Mar in Costa Rica. Breeding male often advertises flower-centred territories by complex, warbling song. Nest undescribed.

Movements. Following breeding, at least part of population descends to lower elevations, regularly to 400-600 m.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Costa Rica and Panama Highlands EBA. Locally very common. Large areas of its wet subtropical forest habitat remain, including tracts in several protected areas such as Braulio Carrillo, Tapanti and Amistad National Parks in Costa Rica.

Bibliography. Anon. (1998a), Fogden (1993), Hernández-Baños *et al.* (1995), Monroe (1963), Renjifo *et al.* (1997), Ridgely & Gwynne (1989), Slud (1964), Stattersfield *et al.* (1998), Stiles (1985b, 1985c), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968a).

178. Variable Mountain-gem

Lampornis castaneiventris

French: Colibri à ventre châtain German: Weißkehlnympe Spanish: Colibrí Variable
Other common names: Chestnut-bellied Mountain-gem; Purple-throated Mountain-gem (*calolaemus*); Grey-tailed Mountain-gem (*cinereicauda*); White-throated Mountain-gem (*castaneiventris*)

Taxonomy. *Trochilus* (—?) *castaneiventris* Gould, 1851, Cordillera de Chiriquí, 6000 feet [c. 1830 m], Panama.

Classification much disputed: three essentially parapatric groups with distinct male plumages hybridize to uncertain extent, probably very limited, where their ranges abut; many previous reports of hybrids may refer to young birds. The groups are: purple-throated, blue-tailed *calolaemus* (with *pectoralis* and *homogenes*); white-throated, grey-tailed *cinereicauda*; and white-throated, blue-tailed *castaneiventris*. Racial allocation of purple-throated birds of the Pacific coastal range of S Costa Rica (*calolaemus* or *homogenes*) is uncertain at present. Where white- and purple-throated forms occur on the same slopes, the former tend to occupy higher elevations. Different authors have advocated recognizing one, two (white-throated as opposed to purple-throated races), or three species. Females of all groups are very similar. More study of this complex is needed. Five subspecies recognized.

Subspecies and Distribution.

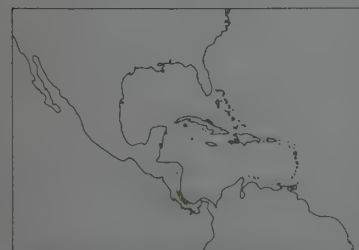
L. c. pectoralis (Salvin, 1891) - extreme S Nicaragua to NC Costa Rica.

L. c. calolaemus (Salvin, 1865) - Cordillera Central and extreme N Cordillera de Talamanca (C Costa Rica).

L. c. cinereicauda (Lawrence, 1867) - Cordillera de Talamanca (S Costa Rica).

L. c. homogenes Wetmore, 1967 - Pacific slope of S Costa Rica (probably) and W Panama.

L. c. castaneiventris (Gould, 1851) - extreme W Panama.



Descriptive notes. 10-11.5 cm; male 5-7-6-2 g, female 4-7-5-1 g. Bill medium-length, straight and black. Male of nominate has crown glittering pale blue-green, gorget white with a few blue or purple feathers along lower margin; conspicuous white postocular stripe; rest of upperparts bright bronzy-green; chest glittering pale green, belly grey, notched tail blue-black. Female lacks bright crown and gorget, entirely cinnamon-rufous below; tail green with blue-black subterminal band and white tips on lateral rectrices. Immature male has crown, throat and chest dull dusky green; young female with rusty fringes on crown and face

feathers. Race *pectoralis* is smaller and darkest below of all races, male with breast glittering dark green; *calolaemus* differs from nominate mainly in purple gorget and turquoise forehead of male; *cinereicauda* similar to nominate but male has forehead turquoise, tail ash grey, and green areas duller and more bronzy in females; *homogenes* is dark below in both sexes. First gorget feathers of

young purple-throated male paler purple to brownish, often with extensive pale bases; of young white-throated male, white to buffy brown, sometimes with faint purplish tinge.

Habitat. Wet subtropical forest (purple-throated races) to colder montane forests, especially of oak (white-throated races). Race *pectoralis* occurs at 800-2000 m; other purple-throated races mostly 1200-2500 m; white-throated races mostly 1850-3000m, in areas where they co-occur, purple-throated and white-throated forms replace each other, more or less abruptly, at elevations below and above c. 2000 m respectively. All forms found mainly in canopy and along edges of mountain forests, with female nesting more in understorey, both sexes occurring down to shrub level at edges and gaps, in adjoining tall second growth, or semi-open and man-made habitats.

Food and Feeding. Male in particular prefers to take nectar at flowers of large epiphytes (*Ericaceae*, *Gesneriaceae*, bromeliads) in middle strata and lower canopy of forest; female more often visits flowers of a variety of shrubs (*Acanthaceae*, *Gesneriaceae*, *Rubiaceae*); both sexes may visit flowers of trees (*Clusia*, *Inga*) or shrubs (*Stachytarpheta*) along edges of coffee plantations or second growth. Aggressive and dominant at flowers, male frequently defending richest clumps. Takes many arthropods, mainly by flycatching, but female in particular often gleans them from foliage, tree trunks, branches and sometimes spiders' webs.

Breeding. Mostly rainy season, Oct-Apr (or June in some forms, notably *pectoralis*). Nest is compact cup of pale or brownish plant down, fine fibres, treefern scales, sprigs of fine liverworts and cobwebs, more or less heavily decorated on outside with bits of moss and lichen, 0.5-3.5 m up in shady forest understorey, usually beside a gap or trail. Clutch size 2; incubation 17-18 days; fledging period 22-23 days.

Movements. Most populations descend to lower elevations following breeding, down to 1200-1500 m (*cinereicauda*) or 300-500 m (*calolaemus*).

Status and Conservation. Not globally threatened. CITES II. Over most parts of range one of the commonest mountain hummingbirds, and protected areas exist in the ranges of all races. The major exceptions are the purple-throated forms of the Pacific slope of S Costa Rica and possibly adjacent Panama, which are poorly known taxonomically and threatened by deforestation; the contact area between *calolaemus* and *cinereicauda* in SC Costa Rica, important for studies on their status, has also been severely deforested. In Costa Rica, has been recorded in several protected areas such as Tapanti National Park and Monteverde Biological Reserve.

Bibliography. Anon. (1998a), Berlioz (1949a), Blake (1958), Feinsinger (1976, 1977, 1980), Feinsinger & Bushy (1987), Feinsinger & Tiebout (1991), Feinsinger, Murray *et al.* (1988), Feinsinger, Tiebout & Young (1991), Feinsinger, Tiebout, Young & Murray (1991), Hartman (1957), Linhart *et al.* (1987), Murray *et al.* (1987), Ridgely & Gwynne (1989), Ridgway (1911), Skutch (1967), Slud (1964), Snow (1977b), Stiles (1985b, 1985c), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968a).

Genus BASILINNA Boie, 1831

179. Xantus's Hummingbird

Basilinna xantusii

French: Saphir de Xantus German: Schwarzstirn-Saphirkolibri Spanish: Colibrí de Xantus
Other common names: Black-fronted Hummingbird

Taxonomy. *Amazilia Xantusii* Lawrence, 1860, near Cape San Lucas, Baja California Sur, Mexico. Genus often merged into *Hylocharis*, though external morphology suggests closer relationship to *Lampornis*. Forms a superspecies with *B. leucotis*. Monotypic.

Distribution. S Baja California; also Cerralvo I and perhaps sporadically on San José I (Gulf of California). Recent vagrant to S California (USA), where attempted to nest.



Descriptive notes. 8-9 cm; 3-2-4-0 g. Male has bill straight, moderately long, red with black tip; head blue-black with white postocular stripe above black auriculars, throat glittering green, breast and belly cinnamon-rufous, nape and back green, wings dusky purple; tail squared, purplish-chestnut with central rectrices edged green. Female duller than male, has bill black above, basally red below; crown dull green instead of black, underparts including throat buffy, eyestripe brown instead of black, bordered above by white postocular stripe; tail mostly rufous but central rectrices green and outer rectrices with dark subterminal

markings and paler tips. Adults are in freshest plumage in northern summer and autumn, duller in spring. Immature male resembles female except for some green on throat.

Habitat. In cape region, occurs in several habitats including oak-pine forest (*Quercus devia*, *Pinus cembroides*) from 1800 to 2200 m in Sierra de La Laguna, and cape deciduous forest, a thorny, heavily grazed association of shrubs, trees and columnar cacti. Fond of water, streams and canyons, therefore usually absent from low elevation desert where *Calypte costae* is seasonally common. Occurs on highest mountains of cape in coldest weather; also in orchards and irrigated shrubbery, sometimes along coast (San José del Cabo, Todos Santos, but not xeric La Paz). On Cerralvo island, prefers higher elevations.

Food and Feeding. In pine-oak forest, the small tubular flowers of madrone trees (*Arbutus peninsularis*) are a critical nectar resource during late winter; other food plants are *Castilleja bryantii*, *Lepechinia hastata*, *Behria tenuiflora*, *Lobelia laxiflora*, *Calliandra peninsularis* and *Mirabilis jalapa*. In cape deciduous forest, visits *Fouquieria diguetii*, which flowers for several months. Gleans insects from pines and oaks.

Breeding. In Sierra de la Giganta, from Feb to at least Apr; nests low in various trees (cottonwood, willow, avocado, lemon). In Sierra de La Laguna, nests Jul-Sept, usually in small oaks. Nest is relatively large, composed of fine plant down, dried flower heads, plant fibres, bark strips, lichens from oaks (when available), bound with spider web. Clutch 2 eggs; incubation 15-16 days by female; fledging period 20-22 days.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Baja California EBA. Occurs almost exclusively in Baja California Sur, where only one other hummingbird species, *Calypte costae*, is present as a potential competitor. Rather versatile in habitat use, although not as well adapted to xeric conditions as is *C. costae*. Considered fairly common to common in cape region in appropriate habitat, more local further north.

Bibliography. Anon. (1998a), Arriaga *et al.* (1990), Banks (1963, 1967), Bent (1940), Brewster (1902), Brown & Bowers (1985), Bryant (1889), Cody (1983), Davis, J. (1959), Friedmann *et al.* (1950), Grinnell (1928), Hainebach (1992), Howell & Webb (1995a), Johnsgard (1997), Lamb (1925), Mayr & Short (1970), Ridgway (1911), Small (1994), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Wagner (1946a), Wiggins (1960), Wilbur (1987).

180. White-eared Hummingbird

Basilinna leucotis

French: Saphir à oreilles blanches

Spanish: Colibrí Orejiblanco

German: Purpurstirn-Saphirkolibri

Taxonomy. *Trochilus leucotis* Vieillot, 1818, Brazil; error = Orizaba, Veracruz.

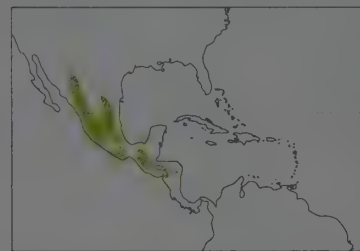
Genus often merged into *Hylocharis*, though external morphology suggests closer relationship to *Lamprolaima*. Forms a superspecies with *B. xantusii*. Three subspecies recognized.

Subspecies and Distribution.

B. l. borealis (Griscom, 1929) - N Mexico (Sonora, Chihuahua, Tamaulipas); rarely to SW USA (SE Arizona).

B. l. leucotis (Vieillot, 1818) - highlands of C & S Mexico to Guatemala.

B. l. pygmaea Simon & Hellmayr, 1908 - highlands of El Salvador, Honduras and Nicaragua.



Descriptive notes. 9-10 cm; male c. 3-6 g, female c. 3-2 g. Male has straight bill, red, tipped black; forehead glittering violet, white postocular stripe, auriculars blackish, rest of upperparts green with lower back and upper-tail-coverts fringed rufous; chin glittering violet, gorget iridescent turquoise green, rest of underparts greyish-green; tail slightly forked, central rectrices green, outer blackish, tipped green. Female has straight bill, upper mandible black, lower red, tipped dark; crown brownish-green, white postocular stripe, auriculars blackish, rest of upperparts green, lower back and uppertail-coverts fringed rufous; throat white with green discs, rest of underparts whitish mottled green; tail centrally green, outer rectrices fringed brown and tipped white. Immature resembles adult female, has rectrices largely tipped white. Race *borealis* is larger, underparts greyer, less green; *pygmaea* is smaller, green gorget smaller, underparts whitish heavily mottled green, tail greenish with rufous fringes.

Habitat. Pine-oak forest, pine-evergreen forest, clearings, at 1200-3500 m. Forages in low to middle strata.

Food and Feeding. Feeds on nectar of flowering *Agave*, *Bidens*, various *Salvia* species, *Penstemon*, *Cuphea* and others. Arthropods are caught in the air by hawking and extracted from flowers. Territorial.

Breeding. Mar-Aug in N & C Mexico; May-Aug and Nov-Feb, possibly all year round, in S Mexico; Aug-Dec for race *pygmaea*. Cup-shaped nest is built out of soft plant down, mainly downy fibres from oak leaves and moss, exteriorly decorated with greyish lichens, placed 1-6-6 m above ground preferably in oak (Mexico) or *Baccharis vacinoides* (Guatemala). Sometimes several nests are built within a short distance of each other; often built on previous year's nest. Clutch size 2; incubation 14-16 days by female; fledging at 23-28 days. Up to 3 broods may be raised in Mexico, 2 in other areas.

Movements. Some migratory activity in northern part of range, where species is most abundant from Apr to Oct, after which not recorded in USA, while in N Mexico less numerous between Nov and Mar. Southern population shows no migratory activity, although some altitudinal dispersal after breeding and following flowering plants may occur.

Status and Conservation. Not globally threatened. CITES II. Common and widespread throughout much of range. No immediate threat recorded; however, parts of its forest habitat are under threat of deforestation; accepts disturbed areas such as clearings.

Bibliography. Amadon & Eckelberry (1955), Arizmendi *et al.* (1996), Baeppler (1962), Baitech & Harrison (1997), Bent (1940), Binford (1989), Cottam & Knappen (1939), Davis (1953), DeGraaf & Rappole (1995), Des Granges (1979), Des Granges & Grant (1980), Desselberger (1932), Dickey & van Rossem (1938), Edwards & Lea (1955), Ely (1962), Friedmann *et al.* (1950), Greenberg *et al.* (1993), Griscom (1934), Hejl *et al.* (1995), Howell & Webb (1995a), Hubbard (1978), Johnsgard (1997), Kaufman (1996), Lea & Edwards (1950), Lyon (1976), Lyon & Chadek (1971), Martínez del Río & Eguarte (1987), Mayr & Short (1970), Monroe (1968), Moore (1939c), Ranta (1986), Ridgway (1911), Rowley (1966, 1984), Russell (1964), Schaldach (1963), Skutch (1935, 1945, 1951, 1972, 1976), Stotz *et al.* (1996), Sutton & Burleigh (1940), Udvardy (1983), Wagner (1942, 1946a, 1957b, 1959).

Genus LAMPROLAIMA Reichenbach, 1854

181. Garnet-throated Hummingbird

Lamprolaima rhami

French: Colibrí à gorge grenat

German: Granatkehlkolibri

Spanish: Colibrí Alicastaño

Taxonomy. *Ornismya Rhami* Lesson, 1838, Mexico.

Possibly belongs in *Basilinna*. Proposed races *occidentalis* (Guerrero) and *saturation* (Honduras and N El Salvador) based on colour and size variation, but both patterns are either age-dependent or clinal in character and thus unsuitable criteria for subspecific recognition. Monotypic.

Distribution. C & S Mexico (Guerrero, Puebla and W Veracruz S through Oaxaca to Chiapas) S to Guatemala, El Salvador and Honduras.

Descriptive notes. 12-12.4 cm; 5-6-7-1 g. Male has short straight black bill; upperparts iridescent green, postocular spot white; throat shining rose pink, breast iridescent violet-blue, rest of under-



parts blackish, mottled green on flanks; remiges rufous, tipped dark brown; tail dark purple, outer rectrices finely tipped grey. Female upperparts like male; below dusky grey, usually pinkish dots on throat; tail duller, with white tips to outer rectrices. Immature female similar to adult female but with buff fringes on head feathers; immature male similar to adult female but with darker underparts, buff fringes to bluish chest feathers, and rufous parts on remiges smaller than in adult male.

Habitat. Upper tropical forest, cloudforest, forest edge, pine-oak forest and scrub, at 1200-3000 m on Atlantic and Pacific slope; most numerous at 1500-2300. In Honduras, does not occur below 1600 m. Forages 1-10 m above the ground.

Food and Feeding. Nectar of flowering shrubs, *Inga* and *Erythrina* trees. Insects are caught in the air by hawking. Male occupies feeding territories.

Breeding. Apr-May (Atlantic slope), Dec-Mar (Pacific slope); nests have also been found in Sept. Bulky cup-shaped nest is composed of moss, parts of leaves, and pine needles, lined with soft plant fibre, attached to roots in banks of washed-out creek beds. Clutch size 2, incubation by female. No further information.

Movements. Sedentary; birds move to higher altitudes (above 1500 m) during reproduction period.

Status and Conservation. Not globally threatened. CITES II. A locally common bird associated with cloudforest and pine-oak forest; readily accepts modification of habitat by man, if patches of forest remain. Frequently recorded in Sierra de Atoyac (Guerrero), Cerro San Felipe (Oaxaca) and Lagos de Montebello (S Chiapas).

Bibliography. Anon. (1998a), Baeppler (1962), Binford (1989), Friedmann *et al.* (1950), Griscom (1932c, 1934), Howell & Webb (1995a), Johnsgard (1997), Land (1970), Monroe (1968), Phillips (1966), Ridgway (1911), Rowley (1966), Stone (1932), Stotz *et al.* (1996), del Toro (1941), Wagner (1957b), Wetmore (1941).

Genus ADELOMYIA Bonaparte, 1854

182. Speckled Hummingbird

Adelomyia melanogenys

French: Colibrí moucheté

German: Schwarzhörlkolibri

Spanish: Colibrí Jaspeado

Other common names: Pipita

Taxonomy. *Trochilus melanogenys* Fraser, 1840, Bogotá, Colombia.

Systematic position poorly understood; the genera *Phlogophilus*, *Anthocephala* and *Urastictes* have been suggested as close relatives, some authors even considering all four to be congeneric; however, because monophyly of these four is doubtful, the monotypic status of *Adelomyia* is maintained. Seven subspecies recognized.

Subspecies and Distribution.

A. m. aeneosticta Simon, 1889 - N & C Venezuela.

A. m. melanogenys (Fraser, 1840) - Andes of W Venezuela (Mérida) and E Colombia S through E Andes to SC Peru.

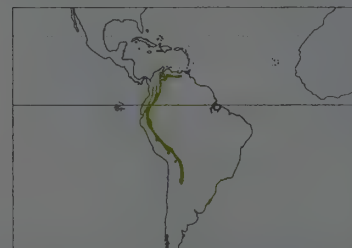
A. m. cervina Gould, 1872 - W & C Andes of Colombia.

A. m. connectens Meyer de Schauensee, 1945 - Huila (S Colombia).

A. m. maculata Gould, 1861 - Ecuador to N Peru.

A. m. chlorospila Gould, 1872 - SE Peru.

A. m. inornata (Gould, 1846) - Yungas of Bolivia and NW Argentina (Salta, Jujuy).



Descriptive notes. 8.5-9 cm; male 4-9 g, female 4-2 g. Sexes alike. Short straight black bill; blackish cheeks, buffy white streak behind the eye; upperparts bronzy-green; speckled dusky on throat, greenish on breast, rest of underparts dull white or buff; tail slightly forked, bronzy-purple, all but the two central rectrices tipped white or buff. Immature with brown fringes on feathers of head and lower back. Race *cervina* larger than nominate, with bill shorter, throat finely spotted brown, underparts richer buff; *connectens* intermediate between *cervina* and *maculata*, tail with small buff tips; *aeneosticta* smaller than nominate.

paler below, speckles restricted to upper throat; *maculata* with large buffy portions on inner webs of tail feathers; *chlorospila* has throat discs deep green; *inornata* with blue discs on throat.

Habitat. Humid forest, forest borders and along watercourses, at 1000-2500 m, commonest around 2000 m. Forages solitarily and rather low down in dense thickets.

Food and Feeding. Nectar of flowering shrubs and vines, including *Lobelia*, *Fuchsia*, *Psammisia*, *Palicourea* and *Bomarea*. Insects are caught by hawking or gleaned from the surface of leaves.

Breeding. Nests have been found all year round, chiefly from Jan to mid-May. Bulky cup-shaped nest of moss and cobweb, lined with fine plant fibre, is built on moss-covered trunks or on rocky ridges, occasionally at the entrance of caves, at height of 1-3 m. Clutch size 2; incubation 17-18 days, by female; chick is blackish with pale grey dorsal down; fledging period 20-24 days; young remain with adult female for 3-4 weeks. First breeding in second year.

Movements. Mainly sedentary; individuals may disperse to lower altitudes after the breeding period.

Status and Conservation. Not globally threatened. CITES II. A very common hummingbird of moderate elevations in the Andes. Particularly abundant in the W Andes above Cali (SW Colombia), with densities of at least 10-12 pairs/km². Occurs in Calilegua National Park, Argentina. Trapping for wild bird trade in Colombia and Ecuador was significant until the mid-1970's but has now apparently ceased.

Bibliography. Aveledo & Pérez (1994), Baez *et al.* (1997), Berlioz (1932d), Best & Clarke (1991), Best *et al.* (1997), Blendinger (1998), Bloch *et al.* (1991), Bond & Meyer de Schauensee (1943), Butler (1979), Canevari *et al.* (1991), Carter (1982), Elgar (1982b), Fjeldså & Krabbe (1990), Fjeldså & Mayer (1996), Fritsch & Schuchmann

(1988), Hilty & Brown (1986), Meyer de Schauensee & Phelps (1978), Miller (1963), Narosky & Yzurieta (1993), Navas (1968), Parker *et al.* (1982), de la Peña (1994), Ridgely & Gaulin (1980), Schäfer & Phelps (1954), Snow & Snow (1980), Stotz *et al.* (1996), Taczanowski (1884), Traylor (1958a), Wetmore (1939), Williams & Tobias (1994), Zimmer (1951a).

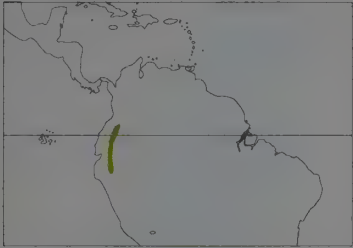
Genus *PHLOGOPHILUS* Gould, 1860

183. Ecuadorian Piedtail

Phlogophilus hemileucurus

French: Colibri à queue mi-blanche **Spanish:** Colibrí Colipinto Ecuatoriano
German: Schwarzweißschwanz-Kolibri

Taxonomy. *Phlogophilus hemileucurus* Gould, 1860, banks of Río Napo, east Ecuador. Has occasionally been placed in genus *Adelomyia*; more information required to permit accurate assessment of most appropriate generic placement. Forms a superspecies with *P. harterti*. Monotypic. **Distribution.** S Colombia (W Putumayo) through E Ecuador to NE Peru (San Martín).



Descriptive notes. 7.3-7.6 cm; 2.2-3 g. Sexes alike. Short straight black bill, yellowish at base; crown greenish-brown, postocular spot white, rest of upperparts grass green; throat and breast white, spotted with green, white band across centre of breast, belly whitish; tail roundish, central pair of rectrices blue-green, remainder blue, white at base and broadly tipped white. Immature like adult but with buff fringes on head and neck feathers. **Habitat.** Forest edge and second growth in Andean foothills at 500-1200 m. Forages in low to middle strata, 2-4 m.

Food and Feeding. Nectar of flowering Rubiaceae, Ericaceae (especially *Psanmisia*), Gesneriaceae. When visiting flowers birds cling to corollas. Insects are mainly gleaned from the surface of plants. **Breeding.** Dec-Apr. Tiny cup-shaped nest of fine rootlets and pieces of fern leaf is built 2-3 m above ground in vines or underneath dense thickets overhanging steep roadsides. Clutch size 2; incubation by female. No further information. **Movements.** Sedentary, local altitudinal movements likely. **Status and Conservation.** Not globally threatened. CITES II. Currently considered Near-threatened. Restricted-range species: present in Ecuador-Peru East Andes EBA. Patchily distributed but common. Readily takes to altered habitat as long as forest patches and thickets of secondary growth remain. **Bibliography.** Balchin & Toyne (1998), Best *et al.* (1997), Butler (1979), Elgar (1975), Fitzpatrick & Willard (1982), Hilty & Brown (1986), King (1991), Meyer de Schauensee (1982), Olrog (1968), Parker & Parker (1982), Parker *et al.* (1982), Rahbek *et al.* (1995), Salaman & Mazariegos (1998b), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Williams & Tobias (1994), Zimmer (1951a).

184. Peruvian Piedtail

Phlogophilus harterti

French: Colibri de Hartert **German:** Hartertkolibri **Spanish:** Colibrí Colipinto Peruano

Taxonomy. *Phlogophilus harterti* Berlepsch and Stolzmann, 1901, Huanaypata, Peru. Has occasionally been placed in genus *Adelomyia*; more information required to permit accurate assessment of most appropriate generic placement. Forms a superspecies with *P. hemileucurus*. Monotypic. **Distribution.** C & SE Peru (S Huánuco, Pasco, Cuzco, Puno). **Descriptive notes.** 7.2-7.5 cm; 2.2-2.7 g. Sexes alike. Short straight black bill; upperparts green; throat and centres of breast and belly white, rest pale buff; tail roundish, central rectrices green, broadly tipped black, rest of rectrices buff with broad black diagonal band. Immature similar to adult but with buff fringes on feathers of head and neck. **Habitat.** Forest edge and secondary growth in Andean foothills at 900-1200 m, most numerous around 1000 m.



erally common in Andean foothills. Readily accepts modification of habitat by man, as long as patches of forest and secondary growth remain. A little-studied hummingbird. **Bibliography.** Meyer de Schauensee (1982), Olrog (1968), Parker *et al.* (1982), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Zimmer (1951a).

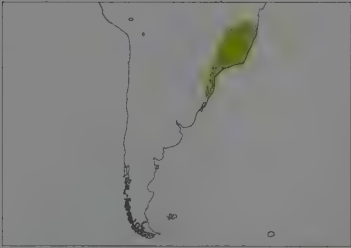
Genus *CLYTOLAEMA* Gould, 1853

185. Brazilian Ruby

Clytolaema rubricauda

French: Colibri rubis-émeraude **German:** Rubinkolibri **Spanish:** Colibrí Colirrojo

Taxonomy. *Trochilus rubricauda* Boddaert, 1783, Rio de Janeiro, Brazil. Sometimes placed in genus *Heliodoxa*; relationships unclear. Monotypic. **Distribution.** E Brazil, from Goiás through S Minas Gerais and Espírito Santo to Rio de Janeiro, São Paulo, Paraná, Santa Catarina and Rio Grande do Sul.



Descriptive notes. 10.8-11.3 cm; male 8.6-9.2 g, female 5.9-7.1 g. Melanistic individuals frequently occur. Male has medium-sized black bill; forehead and crown iridescent emerald green, nape green, rest of back golden bronze, postocular spot white; chin blackish, throat shining ruby red, breast iridescent emerald green, belly dark grey with green-centred feathers; inner rectrices golden bronze, rest rufous, edged bronze. Female grass green above, postocular spot white; below uniformly cinnamon. Immature similar to female, head feathers with buff fringes. **Habitat.** Forest interior, scrub, parks and banana plantations of the central Brazilian and Atlantic regions from sea-level to 1000 m, most numerous below 500 m. **Food and Feeding.** Nectar of native and introduced flowering shrubs, vines and trees, including *Helicteris*, *Dombeya*, *Citrus*, *Genipa*, *Musa*, *Eucalyptus* and *Inga*. Insects are caught in the air by hawking. Male, and to a lesser extent female defend feeding territories. **Breeding.** Nov-Mar. Cup-shaped nest of soft plant material, externally decorated with grey-green lichen, built on horizontal branch 3-10 m above ground. Clutch size 2; incubation 15-16 days, by female; chick black with sparse buff dorsal down; fledging at 25 days. First breeding in second year. **Movements.** Sedentary, locally with some seasonal altitudinal dispersal. **Status and Conservation.** Not globally threatened. CITES II. Common throughout range, and readily accepts man-made habitats like tree-filled gardens, parks and plantations. Occurs in several protected areas, such as Serra dos Órgãos and Itatiaia National Parks (Rio de Janeiro) and Nova Lombardia Biological Reserve (Espírito Santo). **Bibliography.** Belton (1984), Forrester (1993), Gonzaga *et al.* (1995), Grantsau (1988), Guix *et al.* (1992), Oniki (1996), Parker & Goerck (1997), do Rosário (1996), Ruschi (1949b, 1973d, 1981-1982, 1982a, 1986), Sargeant (1996), Sazima, I. *et al.* (1996), Sazima, M. *et al.* (1994), Scott & Brooke (1985), Sick (1993, 1997), Snow & Snow (1986), Snow & Teixeira (1982), Stotz *et al.* (1996), Tobias *et al.* (1993), Willis (1992).



PLATE 61

inches 2
cm 5

Genus *HELIODOXA* Gould, 1849

186. Gould's Jewelfront

Heliodoxa aurescens

French: Brillant à bandeau bleu

Spanish: Brillante Pechicastaño

German: Rotbrustbrilliantkolibri

Other common names: Jewelfront

Taxonomy. *Trochilus (Lampornis) aurescens* Gould, 1846, locality unclear (N Brazil and E Peru both suggested).

Until recently, often placed in monotypic genus *Polyplancta*, but morphological and behavioural parallels, supported by genetic analysis, suggest that species belongs in *Heliodoxa*; probably closely related to *H. schreibersii*. In past, occasionally placed in *Clytolaema*. Despite fairly extensive range, species shows only slight degree of variation. Monotypic.

Distribution. S Venezuela (S Amazonas, Bolívar) through Amazonian Colombia (W Putumayo, Vaupés, Amazonas), E Ecuador and E Peru (S to Puno) to N Bolivia (Pando, Beni, Cochabamba) and NW Brazil (Amazonas and S Pará possibly to R Madeira and N Mato Grosso).

Descriptive notes. 11-12 cm; c. 6.3 g. Bill straight, dark-coloured. Male with narrow frontlet glittering purplish-blue, upperparts shining grass green; underparts with chin, lores and upper throat velvety black, sides of neck and lower throat glittering golden green, bordered by a broad orange-rufous breast band, rest of underparts shining green; tail forked, central pair of tail feathers bronze-green, rest chestnut-edged and tipped bronze-green. Female similar but with crown green, chin feathers tipped buff; also generally duller in coloration with the throat greyish with green discs; short buff to chestnut malar stripe.

Habitat. Understorey of humid forest, especially near creeks and damp places, only rarely at forest edge; frequently in sandy areas, sometimes in *várzea* forests. Found in tropical lowlands at elevations between 150 and 400 m, only occasionally up to 600 m.

Food and Feeding. Mainly feeds on nectar of flowering shrubs but also takes insects in the air by hawking.

Breeding. Jun-Sept. Clutch size 2; incubation by female. No further information.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Generally varies from uncommon to locally common over its fairly sizeable range. Quickly accepts man-made habitats. Present in Tambopata Reserve, Peru.

Bibliography. Brown & Bowers (1985), Butler (1979), Cotton (1998a), Donahue (1994), Fitzpatrick & Willard (1982), Gerwin & Zink (1989), Gilliard (1941), Grantsau (1988), Hilty & Brown (1986), Meyer de Schauensee & Phelps (1978), Parker *et al.* (1985), Ruschi (1981-1982, 1986), Schmitt & Schmitt (1987), Schuchmann (1984b), Sick (1993, 1997), Stotz, Fitzpatrick *et al.* (1996), Stotz, Lanyon *et al.* (1997), Terborgh *et al.* (1984), Willard *et al.* (1991), Zimmer (1951a).

187. Fawn-breasted Brilliant

Heliodoxa rubinoides

French: Brillant rubinoïde

Spanish: Brillante Pechigamuza

German: Braunbauch-Brilliantkolibri

Other common names: Penny-throated/Lilac-throated Hummingbird, Lilac-breasted Brilliant

Taxonomy. *Trochilus rubinoides* Bourcier and Mulsant, 1846, Colombia.

Three subspecies recognized.

Subspecies and Distribution.

H. r. rubinoides (Bourcier & Mulsant, 1846) - C & E Andes of Colombia.

H. r. aequatorialis (Gould, 1860) - W slope of Andes in Colombia and Ecuador.

H. r. cervinularis (Salvin, 1892) - E slope of Andes in Ecuador and Peru.

Descriptive notes. 11-13 cm; 7.3-8.1 g. Bill straight, thick, black. Male shining bronzy-green above turning coppery on wing-coverts; below cinnamon-buff with green chin, green discs on throat and flanks and small rosy violet patch on centre of lower throat; tail is coppery green and slightly forked. Female resembles male but lacks glittering throat patch and green chin. Race *aequatorialis* differs from nominate in more golden green plumage, underparts more strongly spotted with green; *cervinularis* larger, has underparts almost entirely cinnamon-buff with fewer interspersed green discs, throat patch slightly smaller and paler.

Habitat. Understorey of wet and humid pre-montane forest, also along shady borders and forest edges; occasionally in more open habitats like pastures and gardens and in vicinity of towns, at altitudes of 1670-1830 m, locally and seasonally up to 2600 m. Records from Magdalena Valley suggest movements to lower elevations of 1000 m.

Food and Feeding. Takes nectar from a variety of food plants such as *Inga* and *Erythrina*; has been observed flycatching 3-6 m above ground.

Breeding. Jan-May (*rubinoides*, Colombia) or Sept-Jan (*aequatorialis*, Ecuador). Clutch size 2; incubation by female. First breeding in second year. No further information.

Movements. Sedentary with local altitudinal movements.

Status and Conservation. Not globally threatened. CITES II. Uncommon and local. Abundant above Cali (SW Colombia) with recorded densities of at least 3 pairs/km². Regularly reported from area between Nono and Mindo (NC Ecuador).

Bibliography. Best *et al.* (1997), Brown & Bowers (1985), Butler (1979), Chapman (1917, 1926), Davies *et al.* (1994), Fjeldså & Krabbe (1990), Gerwin & Zink (1989), Hilty (1985), Hilty & Brown (1986), Miller (1963), Parker & O'Neill (1980), Parker, Parker & Plenge (1982), Parker, Schultenberger *et al.* (1985), Rasmussen *et al.* (1996), Renjifo *et al.* (1997), Ruschi (1964b), Salaman & Mazariegos (1998b), Stotz *et al.* (1996), Williams & Tobias (1994), Zimmer (1951a).

188. Violet-fronted Brilliant

Heliodoxa leadbeateri

French: Brillant à front violet

Spanish: Brillante Frentivioleta

German: Violetstirn-Brilliantkolibri

Other common names: Blue-crowned Brilliant

Taxonomy. *Trochilus Leadbeateri* Bourcier, 1843, Caracas, Venezuela.

Apparently closest to *H. jacula*. An intergeneric hybrid has been recorded between present species and *Helianthangelus clarisse*. Four subspecies recognized.

Subspecies and Distribution.

H. l. leadbeateri (Bourcier, 1843) - N Venezuela in coastal mountains in Falcón, Yaracuy, Carabobo and Miranda.

H. l. parvula Berlepsch, 1887 - NW Venezuela (Táchira, Mérida, Barinas, Trujillo) and N. C & S Colombia (Serranía de Perijá and E Andes S to Macarena Mts, locally in Magdalena and Cauca Valleys, and possibly also N end of C Andes).

H. l. sagitta (Reichenbach, 1854) - E Ecuador and N Peru.

H. l. otero (Tschudi, 1844) - C & S Peru and NW Bolivia.

Descriptive notes. 11-13 cm; male 7.5-8.5 g, female 6.6-7.5 g. Bill almost straight, blackish. Male bronze-green above turning coppery on neck, forehead glittering blue; faint white malar streak and small white spot behind eye; underparts with glittering emerald green gorget, lower breast and belly dull bronze-green; tail deeply forked; central pair of rectrices bronze-green, next pair steel blue, tipped bronze, remainder entirely dark steel blue. Female has forehead glittering green, otherwise coppery green above; short white malar streak and small white spot behind eye; throat and breast thickly spotted with glittering green discs; underparts

mainly white turning buffy towards belly; tail shorter and less deeply forked than in male and feathers with narrow white tips. Race *parvula* differs in having frontal patch more violet than blue, coloration of belly paler and duller, central pair of tail feathers lighter and greener, the rest more blackish, and female with belly more cinnamon-buff; *sagitta* has a strong blue frontal patch, underparts and central rectrices resemble previous race in coloration, breast often with a bluish hue, female with belly almost whitish and a blue patch on crown; male *otero* has upperparts less coppery, female differs in having brownish belly, and lacks glittering green frontlet almost completely. **Habitat.** Pre-montane rainforest and cloudforest and forest edge, occasionally also scrub, small clearings, low open woodland, second growth, or coffee plantations. Mainly upper tropical and subtropical zones, but may sometimes ascend to lower border of temperate zone. Altitudinal distribution ranges from 400 to 2400 m. Replaced at lower elevations by *H. jacula*.

Food and Feeding. Takes nectar mainly at flowers in lower to middle strata (1-10 m) inside forest or near small openings at forest edge. Usually forages alone and does not gather in groups at flowering trees. A substantial part of the diet consists of insects obtained by flycatching.

Breeding. Jan-May. Clutch size 2; incubation by female. No further information.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Reported estimates of abundance are to some extent contradictory, but species appears to be quite common, at least locally. Has been recorded at Henri Pittier National Park (N Venezuela).

Bibliography. Best *et al.* (1997), Bloch *et al.* (1991), Bond & Meyer de Schauensee (1943), Brown & Bowers (1985), Butler (1979), Chapman (1917, 1926), Collins (1972b), Davies *et al.* (1994), Fjeldså & Krabbe (1990), Gerwin & Zink (1989), Graves & Zusi (1990a), Hilty & Brown (1986), Meyer de Schauensee & Phelps (1978), Parker *et al.* (1982), Remsen & Traylor (1989), Ridgely & Gaulin (1980), Rutgers & Norris (1972), Salaman & Mazariegos (1998a, 1998b), Stotz *et al.* (1996), Williams & Tobias (1994), Zimmer (1930, 1951a).

189. Velvet-browed Brilliant

Heliodoxa xanthogonys

French: Brillant à couronne verte

German: Grüner Brilliantkolibri

Spanish: Brillante de Tepui

Taxonomy. *Heliodoxa xanthogonys* Salvin and Godman, 1882, Merumé Mountains, Guyana.

Southern populations apparently represent a separate race; scientific description currently in preparation. Monotypic.

Distribution. Highlands and tepuis of S & E Venezuela, Guyana and NC Brazil.

Descriptive notes. 10-11 cm; 7.0 g. Bill straight, blackish above, lower mandible reddish with dark tip. Male has forehead and centre of crown glittering golden green to emerald green; supercilium velvet blackish; rest of crown, auricular area, hindneck and upperparts to rump dark golden green; throat glittering turquoise to golden green, with glittering violet-blue patch on upper throat; belly dark golden green; uppertail-coverts and median rectrices bronze-green to emerald green; outer rectrices blackish-green; undertail-coverts greenish, narrowly edged greyish and rufous. Female is generally lighter in coloration; forehead and crown rarely glittering, lacks black supercilium; white moustachial streak; below, whitish with greenish spots; lacks violet throat patch; small white breast patch; lower belly whitish; rectrices tipped white; undertail-coverts greyish-brown. Immature male has dark green crown with rufous borders, lacks glittering forehead; throat patch reduced or lacking; generally, underparts, especially centres of throat and belly, more greyish-brown.



Habitat. Forest, forest edges, clearings and scrub within the sub-montane zone of *cerros* and *tepuis* of the Pantepui region; mostly at 700–2000 m.

Food and Feeding. Nectar of various plants such as *Tyleria* and insects.

Breeding. Saddle-type nest; clutch size 2. No further information.

Movements. Probably almost sedentary. As the species has not been recorded from the lowlands of southern Venezuela, seasonal movements may be only altitudinal.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species:

present in Tepuis EBA. As an endemic of the Pantepui region, it can be regarded as an insular species with a remarkably scattered distribution, including Duida-Marahuaca and Serranía de la Neblina National Parks (Venezuela/Brazil). Although not recorded in large numbers within the Pantepui region, species seems to be locally abundant. Precise limits of distribution remain uncertain, as data gaps still exist in areas with suitable habitat that are partly unexplored; for example, extent of range in Brazil is unclear.

Bibliography. Barrowclough, Escalante *et al.* (1997), Barrowclough, Lentino & Sweet (1997), Chapman (1931), Chubb (1916), Cory (1918), Forrester (1993), Friedmann (1948), Gerwin & Zink (1989), Grantsau (1988), Mayr & Phelps (1967), Meyer de Schauensee & Phelps (1978), Ruschi (1981–1982, 1986), Sánchez (1995), Sick (1993, 1997), Snyder (1966), Stattersfield *et al.* (1996), Stotz *et al.* (1996), Warren (1966), Willard *et al.* (1991).

190. Black-throated Brilliant

Heliodoxa schreibersii

French: Brillant à gorge noire

Spanish: Brillante Ventrinegro

German: Schwarzkehl-Brillantkolibri

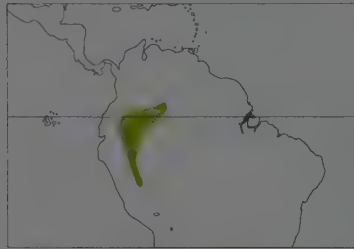
Taxonomy. *Trochilus Schreibersii* Bourcier, 1847, upper Rio Negro, Brazil.

Formerly isolated in monospecific genus *Ionolaima*. Probably closely related to *H. aurescens*. Two subspecies recognized.

Subspecies and Distribution.

H. s. schreibersii (Bourcier, 1847) - SE Colombia, E Ecuador and NE Peru (N of Amazon) to extreme NW Amazonian Brazil (upper R Negro).

H. s. whitelyana (Gould, 1872) - E Peru.



Descriptive notes. 12 cm; male 9.9 g, female 7.1–8.5 g. Bill almost straight and dark in colour. Male has forehead glittering green, crown and rest of upperparts shining green; underparts black with a glittering purple spot on lower throat, bordered below by a narrow band of glittering green; tail very long, deeply forked, steel blue. Female resembles male but has whitish to rufous malar stripe; underparts grey with bronze-green discs and central tail feathers green; tail less deeply forked. Immature resembles female, but malar stripe more deeply coloured. Race *whitelyana* lacks glittering green frontlet and green breast band.

Habitat. Interior of tall humid forest and scrub in tropical and upper tropical zones at elevations between 400 and 1000 m, occasionally up to 1300 m.

Food and Feeding. Forages mainly at heights of about 2–4 m in shady understorey. Feeds on nectar of flowering plants like Ericads. Insects are caught in the air by hawking.

Breeding. Feb–May. Clutch size 2; incubation by female. No further information.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Seems to be rather uncommon, but scarcity of reliable data concerning abundance makes overall assessment difficult. Recorded in Manu National Park, Peru.

Bibliography. Best *et al.* (1997), Butler (1979), Cardiff (1983), Fitzpatrick & Willard (1982), Forrester (1993), Gerwin & Zink (1989), Grantsau (1988), Hilty & Brown (1986), Meyer de Schauensee (1982), Parker *et al.* (1982), Ruschi (1981–1982, 1986), Salaman & Mazariegos (1998b), Schulenberg *et al.* (1984), Sick (1993, 1997), Stotz *et al.* (1996), Zimmer (1951a).

191. Pink-throated Brilliant

Heliodoxa gularis

French: Brillant à gorge rose

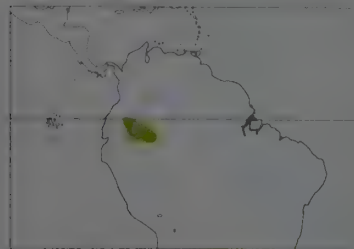
German: Rotkehl-Brillantkolibri

Spanish: Brillante Gorgirrosado

Taxonomy. *Aphantochroa* ? *gularis* Gould, 1860, Río Napo.

Formerly isolated in monospecific genus *Agapeta*. Probably closely related to *H. branickii*. Monotypic.

Distribution. E Andean foothills of S Colombia, NE Ecuador, NE Peru and extreme NW Brazil.



Descriptive notes. 11–12 cm. Male has almost straight black bill; shining green upperparts with glittering green median stripe on forehead, postocular spot small, white; shining green below, throat with glittering pinkish-red patch, belly grey, undertail-coverts whitish; tail long, forked, bronzy-green. Female similar to male, throat patch smaller.

Habitat. Humid montane forest at 400–900 m, possibly higher.

Food and Feeding. Almost no food plants have been recorded apart from flowering *Psittacanthus* and other Loranthaceae; takes insects.

Breeding. No data available.

Movements. Presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Currently considered Near-threatened. Restricted-range species: present in Ecuador–Peru East Andes EBA. Generally uncommon. Forest habitat within range is under threat of destruction. Species very poorly known; extensive research required.

Bibliography. Best *et al.* (1997), Butler (1979), Fitzpatrick & Willard (1982), Forrester (1993), Gerwin & Zink (1989), Grantsau (1988), Hilty & Brown (1986), Parker *et al.* (1982), Ruschi (1981–1982, 1982a, 1986), Salaman & Mazariegos (1998b), Sick (1993, 1997), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Taczanowski (1984), Zimmer (1951a).

192. Rufous-webbed Brilliant

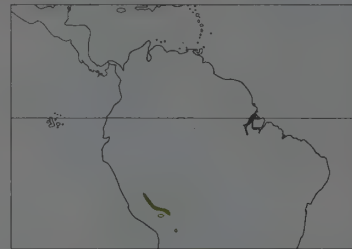
Heliodoxa branickii

French: Brillant de Branicki German: Rotflügel-Brillantkolibri Spanish: Brillante Alicanela

Taxonomy. *Lampraster branickii* Taczanowski, 1874, Monterico, Peru.

Formerly isolated in monospecific genus *Lampraster*. Probably closely related to *H. gularis*. Monotypic.

Distribution. SE Peru and probably NW Bolivia.



Descriptive notes. 11–12 cm; 5.1–5.9 g. Bill straight, black; in male, lower mandible partly whitish. Male has glittering crown, changing from green at bill to more bluish towards rear, rest of upperparts shining dark green; central pair of rectrices green, rest dark blue; underparts green with a glittering iridescent rosy patch at centre of throat, undertail-coverts white; the outer web of the outer remiges and the basal parts of the inner ones are a conspicuous cinnamon-rufous, tail slightly forked. Female above similar to male, head with small white streak below eye; throat green with white spot, breast and belly white to buffy inter-spersed with shining green, and with shining green sides and flanks; undertail-coverts white, tail colour similar to male, central rectrices tipped white, tail slightly forked.

Habitat. Forest, forest edge, woodland and also plantations in mainly Andean foothills at elevations of 750–1300 m.

Food and Feeding. Feeds largely on nectar. Proportion of diet consisting of insects has not yet been investigated.

Breeding. Unknown.

Movements. No information available.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Peruvian East Andean Foothills EBA. The biology of this species has not yet been investigated, in part because its range is very poorly known, so an assessment of abundance or population trends is not possible; however, its acceptance of man-made habitats suggests that it is not under serious threat at present. Occurs between Cuzco and Manu, Peru.

Bibliography. Gerwin & Zink (1989), Meyer de Schauensee (1982), Olrog (1968), Parker *et al.* (1982), Remsen & Traylor (1989), Sagot (1998b), Schulenberg *et al.* (1984), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Zimmer (1930, 1951a).

193. Empress Brilliant

Heliodoxa imperatrix

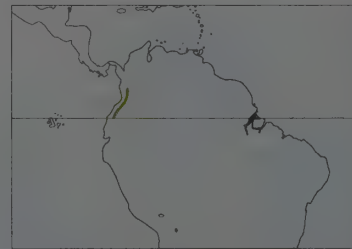
French: Brillant impératrice German: Rotstern-Brillantkolibri Spanish: Brillante Emperador

Other common names: Empress Eugenie's Hummingbird

Taxonomy. *Eugenia imperatrix* Gould, 1856, Andean forests in the neighbourhood of Quito (probably Pacific slope).

Long segregated in monospecific genus *Eugenia* on the basis of its long, very deeply forked tail. Monotypic.

Distribution. Pacific slope from WC Colombia to NW Ecuador.



Descriptive notes. Male 15–17 cm, 9.3 g; female 12–13.5 cm, 8.3 g. Bill black, feet dusky grey; tail quite variable in length, especially among adult males. Male with frontlet, lores, throat and breast glittering dark green, square patch of glittering pale violet on centre of throat, belly glittering golden green; crown and nape dark green, rest of upperparts dark bronzy-green, central rectrices dark bronze, elongated lateral rectrices black, glossed with bronze. Female is bronzy-green above and on central rectrices, lateral rectrices dull black glossed with bronze; centre of throat and breast greyish, heavily flecked with bronzy-green,

passing to solid bronzy-green laterally and to golden green on belly. Immature male with head, throat and breast dull, dark bronzy-green, centre of throat dusky grey; lores, chin and sides of throat bright buff; golden green of belly duller and bronzier, tail shorter than adult. Immature female has throat buffy like male, green feathers below with buffy fringes and duller than adult.

Habitat. Very wet foothills and lower mountain cloudforest and forest edge, adjacent tall second growth, at 400–2000 m. Both sexes occur in canopy of forest and lower down along edges; only female usually seen in understorey.

Food and Feeding. Regularly visits inflorescences of *Marcgravia* and *Marcgraviastrum*, perching on inflorescence to extract nectar from bracts; hovers to feed from pendent blossoms of epiphytic Ericaceae. Little information on foraging for arthropods; has been observed gleaning and flycatching at lower and middle strata in forest.

Breeding. Jan–Apr (W Colombia). One nest (perhaps incomplete) was a downy cup of balsa floss and cobweb, plastered on top of palm frond 10 m up at forest edge. No further information.

Movements. No information.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Chocó EBA. Uncommon to locally common in Colombia, its very wet forest habitat still mostly intact, including several protected areas such as Tatamá, Munchique and Farallones de Cali Na-

tional Parks; frequently seen at La Planada Reserve, and also occurs in Rio Nambi Reserve. In Ecuador, regularly recorded in forest around Mindo.

Bibliography. Best *et al.* (1997), Butler (1979), Chapman (1926), Gerwin & Zink (1989), Hilty (1997), Hilty & Brown (1986), Kirwan & Marlow (1996), Meyer de Schauensee (1949, 1982), Olrog (1968), Orejuela *et al.* (1982), Salaman (1996), Salaman & Mazariegos (1998b), Stattersfield *et al.* (1998), Stotz *et al.* (1996).

194. Green-fronted Brilliant

Heliodoxa jacula

French: Brillant fer-de-lance **German:** Grünstirn-Brilliantkolibri **Spanish:** Brillante Coroniverde
Other common names: Green-crowned Brilliant

Taxonomy. *Heliodoxa jacula* Gould, 1850, Santa Fé de Bogotá, Colombia.

Race *jamesoni* often spelt *jamersoni*, due to a typographical error present in original description. Three subspecies recognized.

Subspecies and Distribution.

H. j. henryi Lawrence, 1867 - Costa Rica and W Panama.

H. j. jacula Gould, 1850 - extreme E Panama to N & C Colombia.

H. j. jamesoni (Bourcier, 1851) - SW Colombia and W Ecuador.

Descriptive notes. Male 12-13 cm, 7-9 g; female 10-5-12 cm, 6-8 g; race *henryi*, male 9-4 g, female 8-2 g. Male has forehead, crown, lores, throat and breast glittering dark blue-green, a small metallic violet-blue patch on foreneck, and white postocular spot; rest of upperparts and belly bronzy-green, central rectrices bronzy, rest of deeply-forked tail blue-black. Female lacks glittering areas on head and underparts, has short white malar streak, whitish below very heavily spotted with green; lateral rectrices white-tipped. Immature male dull, dark bronzy-green on crown and underparts with chin and malar area, sometimes entire throat, in striking contrast bright buff; tail shorter and less deeply forked. Immature female has green spotting below duller, throat as young male. Race *henryi* larger, glittering areas of male more brilliant, paler green (little or no bluish tinge), tail of male entirely blue-black, female more extensively white below with bright



Heliconia along streams. Usually perches on inflorescence to feed. Male sometimes defends large clumps of *Marcgravia* or *Heliconia*. Captures arthropods by flycatching and foliage-gleaning.

Breeding. Jul or Aug-Jan (Costa Rica); May-Sept (N & EC Colombia). Nest undescribed.

Movements. In Costa Rica, most of population moves to lower elevations (locally down to 100 m) outside breeding season; no data for other areas.

Status and Conservation. Not globally threatened, CITES II. Common, at least locally, in Costa Rica and Panama (*henryi*), with various protected areas in range, e.g. Tapanti National Park and Monteverde Biological Reserve (Costa Rica). Much less common and more local in Colombia (*jacula*), and in most areas has probably suffered moderate to severe habitat loss due to deforestation; has been recorded in several protected areas, such as Los Katíos National Park and Rio Nambi Reserve. No information available for *jamesoni*.

Bibliography. Anon. (1998a), Best, Checker *et al.* (1996), Best, Heijnen & Williams (1997), Blake (1958), Butler (1979), Chapman (1926), Fjeldså & Krabbe (1990), Fogden (1993), Gerwin & Zink (1989), Hilty & Brown (1986), Pople *et al.* (1997), Ridgely & Gaulin (1980), Ridgely & Gwynne (1989), Ridgway (1911), Rutgers & Norris (1972), Salaman & Mazariegos (1998b), Slud (1964), Stiles (1985b, 1985c, 1995a), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968a), Williams & Tobias (1994).

green spotting laterally; male *jamesoni* much duller green on crown, throat and breast; central rectrices glossed with green, tail shorter.

Habitat. Wet subtropical and cloudforest, forest edge, adjacent semi-open and old second growth in mountains and foothills; mostly in middle strata and canopy of forest, female more in understorey. Mostly at 700-2000 m in Costa Rica, 300-1600 m in Colombia.

Food and Feeding. Regularly takes nectar from pipe-shaped bracts of candelabra-like inflorescences of *Marcgravia*; also feeds at other epiphytes (Ericaceae, Gesneriaceae) and shrubs (*Drymonia*, *Cephaelis*), particularly at



Genus *EUGENES* Gould, 1856

195. Magnificent Hummingbird

Eugenes fulgens

French: Colibri de Rivoli **German:** Violettbron-Brilliantkolibri **Spanish:** Colibrí Magnífico
Other common names: Rivoli's Hummingbird; Admirable/Costa Rica/Panama Hummingbird (*spectabilis*)

Taxonomy. *Trochilus fulgens* Swainson, 1827, Temascaltepec, Mexico. Genus sometimes merged into *Heliodoxa*. Race *spectabilis* may be a separate species, on basis of morphological differences and geographical isolation. Populations within southern portion of range of nominate have been separated as race *viridiceps*, but validity highly dubious and no consistent differences are apparent. Two subspecies currently recognized.

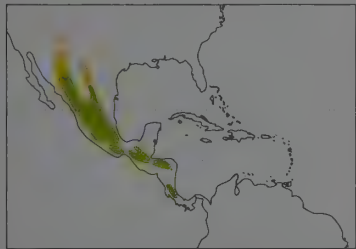
Subspecies and Distribution.

E. f. fulgens (Swainson 1827) - SW USA (SE Arizona, SW New Mexico, SW Texas) through most of Mexico to Guatemala, El Salvador, Honduras and NE Nicaragua.

E. f. spectabilis (Lawrence, 1867) - highlands of Costa Rica and W Panama.

Descriptive notes. 11-13 cm, 7.0-7.5 g; race *spectabilis* 12-14 cm, male c. 10 g, female c. 8-5 g. Male has stout, straight, black bill; iridescent purple crown, small white spot behind the eye, upperparts dark green; green gorget, rest of underparts blackish; tail slightly notched, bronze. Female lacks iridescent gorget, bronze coloration on wings and tail, and has paler, greyish underparts. Immature resembles adult female. Race *spectabilis* rather similar, male with blue-green gorget and somewhat paler underparts.

Habitat. Typically at elevations between 1500 and 2500 m. Sometimes above 3000 m in Costa



Rica, although often moves to lower elevation during colder months. In USA and N Mexico found in mixed Sonoran and upper transitional zones; in S Mexico and Central America in upper arid zones with seasonal rainfall to more humid cloudforests. Common in mixed oak-pine forests near riparian areas. Often frequents open areas where food plants grow.

Food and Feeding. Floral nectars from several plant species, including *Crisium*, *Penstemon*, *Agave americana*, *A. parryi*, *Bomarea costaricensis*, *Centropom talamanensis*, *Erythrina corallodendrum*, *Fuchsia splendens* and *Lobelia laxifolia*. Arthropods taken are primarily insects (beetles, flies, bugs Homoptera, Hymenoptera) and spiders.

Breeding. May-Jul in USA (probably true for all migratory populations); in Central America Nov-Jul with peaks during winter flowering seasons. Nest cup-shaped with soft downy interior, exterior covered by lichen or other similar material. Nest usually placed more than 5 m above ground. Clutch size 2; incubation 15-16 days, by female.

Movements. Populations in N and possibly C Mexico migrate N in late autumn or early spring to extreme N Mexico and SW USA. Populations in S Mexico and Central America are sedentary, although altitudinal migrations can occur during cold seasons.

Status and Conservation. Not globally threatened. CITES II. In USA, artificial feeders maintain unusually large populations that exceed available natural food sources. Susceptible to natural or unnatural perturbations such as forest fires because habitat is often restricted to the higher elevations of isolated mountain ranges. In future, habitat destruction could prove to be a significant threat throughout range. In Costa Rica, occurs in several protected areas such as Volcán Poás National Park and Monteverde Biological Reserve.

Bibliography. Baicich & Harrison (1997), Baker & Blake (1962), Baltosser (1986a), Bené (1947), Bent (1940), Binford (1989), Colwell (1973), Cottam & Knappen (1939), DeGraaf & Rappole (1995), Des Granges (1979), Des Granges & Grant (1980), Dickey & van Rossem (1938), Eisenmann (1955), Ely (1960, 1962), Feinsinger (1980), Friedmann *et al.* (1950), Hainsworth & Wolf (1976, 1978), Hainsworth *et al.* (1981), Hejl *et al.* (1995), Howell & Webb (1995a), Johnsgard (1997), Kaufman (1996), Kuban & Neill (1980), Lasiewski & Lasiewski (1967), Lyon (1976), Lyon & Chadek (1971), Marshall (1957), Martínez del Río & Eguarte (1987), Mayr & Short (1970), Miller (1955), Monroe (1968), Navarro *et al.* (1991), Oberholser (1974), Phillips *et al.* (1964), Pimm (1978), Pimm *et al.* (1985), Powers (1996), Remsen, Stiles & Scott (1986), Ridgely & Gwynne (1989), Ridgway (1911), Rising (1965), van Rossem (1939, 1945a), Rutgers & Norris (1972), Schaldach (1963), Short & Phillips (1966), Slud (1964), Spofford (1980), Stiles (1978a), Stiles & Skutch (1989), Stotz *et al.* (1996), Toledo (1974), Urban (1959), Wagner (1957b), Wetmore (1968a), Wolf (1975a), Wolf *et al.* (1976).

Genus *HYLONYMPHA* Gould, 1873

196. Scissor-tailed Hummingbird

Hylonympha macrocerca

French: Colibrí à queue en ciseaux **German:** Grünbrustnymph **Spanish:** Colibrí Tijereta

Taxonomy. *Hylonympha macrocerca* Gould, 1873, no locality = Cerro Azul, Venezuela.

Genus sometimes merged into *Heliodoxa*. Monotypic.

Distribution. Paria Peninsula (NE Venezuela).

Descriptive notes. Male 19 cm (including 9-10 cm tail), 7-7.5 g; female 12-13 cm, 6-5.8 g. Male has long, slightly decurved black bill; glittering violet cap, covering forehead and centre of crown, rest of crown very dark green, almost black; back slightly metallic grass green with a golden hue on the neck;



throat and breast glittering emerald green, rest of underparts duller and darker green, turning blackish on belly, with green discs on flanks; tail long and deeply forked with lateral feathers much longer and broader than the rest, blackish-purple. Female dark shiny green above, lacking the glittering cap; below white spotted with shiny green discs, but centre of breast without spots, forming a white area; belly and undertail-coverts rufous-chestnut; tail forked but much shorter than in male, central pair of rectrices basally green and distally steel blue, lateral tail feathers cinnamon tipped beige.

Habitat. Mainly damp mossy forest with high trees and cloudforest in subtropical and lower subtropical zone. Also occasionally found at forest edge and small clearings. Records range from altitudes of 900 to 1200 m.

Food and Feeding. Nectar is taken mainly from bromeliads in cloudforest; in secondary growth main food plants are *Heliconia aurea* and *Costus*. Females have been recorded establishing feeding territories. Arthropods are either gleaned from bromeliads or caught in the air by hawking.

Breeding. No information.

Movements. Sedentary.

Status and Conservation. CRITICALLY ENDANGERED. CITES II. Restricted-range species: present in Caripe-Paria Region EBA. Generally rare; endemic to Paria Peninsula. Entire range covered by Paria Peninsula National Park since 1978, but is surrounded with intensive cash-crop cultivation belonging to local farmers. Illegal, uncontrolled burning causes severe damage to remaining forest stands. Due to forest destruction large areas are heavily affected by erosion and drying-up of streams. Less disturbed by humans is the area around Macuro in E because of reduced accessibility by road. Another severe threat is the planned gas pipeline, known as "Proyecto Cristóbal Colón", through the national park. Size of remaining population unknown.

Bibliography. Anon. (1989b), Bond *et al.* (1989), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Knox & Walters (1994), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Olrog (1968), Paynter (1982), Phelps & Phelps (1948, 1958), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Wege & Long (1995).

Genus *STERNOCLYTA* Gould, 1858

197. Violet-chested Hummingbird

Sternoclyta cyanopectus

French: Colibrí à poitrine violette **German:** Veilchenbrustkolibri **Spanish:** Colibrí Pechiazul

Taxonomy. *Trochilus (Lampornis) cyanopectus* Gould, 1846, Neiguata Plantation, near Camburi Grande, La Guaira, Venezuela.

Genus sometimes merged into *Heliodoxa*. Monotypic.

Distribution. N Venezuela, in Andes of Táchira, Mérida and Lara and coastal mountains E to Miranda.



Descriptive notes. 12-13 cm; male 8.4-9.4 g, female 9.0-10.3 g. Bill slightly curved, black. Male shining grass green above; below with throat glittering emerald green, breast with drop-shaped patch of glittering violet-blue; rest of underparts greyish-buff with golden green discs on flanks; tail bronze, the lateral pair of feathers tipped whitish on inner web. Female above like male; underparts greyish-white with golden green discs, towards centre of belly almost entirely rufescent. Immature resembles female.

Habitat. Humid forest and woodland in lower subtropical zone; also found in old second growth and coffee plantations. Occasionally

down to tropical zone, in rainforest and cloudforest. Altitudinal distribution from sea-level to 1900 m.

Food and Feeding. Usually keeps inside dense vegetation and forages in darkest areas of the forest. Often to be found in damp ravines or *Heliconia* thickets. No further information.

Breeding. Clutch size 2; incubation by female. No further information.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Cordillera de la Costa Central EBA and Cordillera de Mérida EBA. Locally common; seems readily to accept second growth and man-made habitats. Occurs in Henri Pittier National Park.

Bibliography. Brown & Bowers (1985), Collins (1972b), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Olrog (1968), Renjifo *et al.* (1997), Rodner (1995), Stattersfield *et al.* (1998), Stotz *et al.* (1996).

Genus *UROCHROA* Gould, 1856

198. White-tailed Hillstar

Urochroa bougueri

French: Colibrí de Bouguer **German:** Blaukehl-Andenkolibri **Spanish:** Colibrí de Bouguer

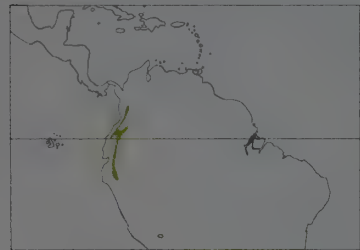
Taxonomy. *Trochilus Bougueri* Bourcier, 1851, Nanegal, Ecuador.

Formerly considered a close relative of *Oreotrochilus*; behaviour and morphology indicate phylogenetic affinities with *Boissonneaua*. Two subspecies recognized.

Subspecies and Distribution.

U. b. bougueri (Bourcier, 1851) - Pacific slope of Andes of SW Colombia and NW Ecuador.

U. b. leucura Lawrence, 1864 - E slope of E Andes in S Colombia (Nariño), E Ecuador and NE Peru.



Descriptive notes. 13-14 cm (including bill 3 cm); 8.5-9.2 g. Sexes alike. Long, straight, black bill; upperparts coppery green, rufous cinnamon malar streak; throat and breast iridescent blue, belly dull grey; central and outermost rectrices black, rest white with dusky grey edges. Immature similar to adult but head feathers with buff fringes. Race *leucura* has bronzy-green upperparts, lacks rufous malar streak; central tail feathers bronzy, others white, dusky grey on outer web.

Habitat. Montane forest, forest edge and secondary growth, especially near streams, at 1600-2800 m, most numerous around 1800 m;

occasionally found on shrubby slopes and at much lower elevations, for example on Pacific slope in SW Colombia. Forages inside forest, usually solitarily, from lowest to middle strata.

Food and Feeding. Nectar of flowering *Inga* trees, *Bomarea*, *Psammisia* and *Cavendishia*. Insects are caught above streams or in forest openings by hawking. Male establishes feeding territories at nectar-rich flower stands, sometimes as low as 1-2 m.

Breeding. Dec-Mar in SW Colombia. Cup-shaped nest of moss and lichen is built on vertical, medium-sized branch of tall tree, often 8-12 m above ground. Clutch size 2; incubation 16-18 days, by female; chick black with sparse buff dorsal down; fledging period 23-25 days.

Movements. Sedentary, with some seasonal altitudinal dispersal, especially on Pacific side of Colombia.

Status and Conservation. Not globally threatened. CITES II. Common in cloudforests and along streams. Accepts man-made habitats, such as pastures, so long as some forested patches remain. Regularly recorded in La Planada Reserve (S Colombia).

Bibliography. Best *et al.* (1997), Butler (1979), Fjeldså & Krabbe (1990), Hilty & Brown (1986), Kirwan & Marlow (1996), Meyer de Schauensee (1982), Olog (1968), Parker *et al.* (1982), Renjifo *et al.* (1997), Salaman & Mazariegos (1998b), Stotz *et al.* (1996).

Genus *BOISSONNEAU* Reichenbach, 1854

199. Buff-tailed Coronet

Boissonneaua flavescens

French: Colibri flavescens **German:** Fahlschwanzkolibri **Spanish:** Colibrí Colihabano

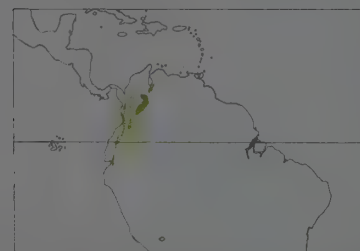
Taxonomy. *Trochilus flavescens* Loddiges, 1832, Popayán, Colombia.

Specimens at the south end of the range of nominate are similar in colour to *tinochlora*, but the subspecific distinction is still evident in the general coloration and the pattern of the tail-feather tips. Two subspecies recognized.

Subspecies and Distribution.

B. f. flavescens (Loddiges, 1832) - Andes of NW Venezuela (Mérida) and Colombia (all three ranges).

B. f. tinochlora Oberholser, 1902 - SW Colombia and W Andean slope of Ecuador.



Descriptive notes. 11-12 cm; 8.0-8.6 g. Bill straight, black. Male shining green above; throat and breast are shining green, remainder of underparts buff strongly marked with green discs, underwing-coverts cinnamon and conspicuous in flight; central pair of feathers in the slightly forked tail bronzy, rest buff with bronzy edges and tips; rather small leg puffs white. Sexes similar, but female has more buffy underparts, shorter wings and tail and narrower bronzy edges and tips of lateral rectrices. Immature like female but with brownish edges to rump feathers. In *tinochlora* the buff parts of plumage have a distinctive cinnamon hue,

bronzy tips to tail feathers are broader than in nominate; in female and immature, tail-feather tips are only slightly narrower than in adult male.

Habitat. Throughout its quite extensive range inhabits humid and wet montane forest, cloudforest and dwarf forest and forest borders, but also open and more shrubby areas in upper subtropical and lower temperate zones, at elevations between 2000 and 3500 m.

Food and Feeding. Usually feeds in middle strata but also occasionally found in canopy. Main food plants are *Cavendishia*, *Palicourea*, *Disterigma* and *Huilaia*. While feeding, typically clings to flowers rather than hovering. Frequently seen hawking for insects in long sallies from high perches, but sometimes also clings to tree trunks when gleaning insects. Has also been observed feeding at sap trees at holes made by woodpeckers. Territorial and pugnacious.

Breeding. Apr-Aug (Colombia) and Nov-Mar. Nest is cup-shaped, built mainly of moss and lichen; usually attached to branch 3-10 m above ground. Clutch size 2; incubation by female. First breeds in second year.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Rare to locally fairly common. Frequently seen along old road to Mindo (W Ecuador), with densities of at least 1-2 pairs/km². Present in La Planada Reserve (S Colombia).

Bibliography. Best *et al.* (1997), Brown & Bowers (1985), Butler (1979), Chapman (1917, 1926), Fjeldså & Krabbe (1990), Hilty & Brown (1986), Kattan & Murcia (1985), Kirwan & Marlow (1996), Meyer de Schauensee (1949, 1982), Meyer de Schauensee & Phelps (1978), Miller (1963), Olog (1968), Ridgely & Gaultin (1980), Salaman & Mazariegos (1998b), Snow & Snow (1980), Stotz *et al.* (1996), Vélez & Velázquez (1998).

200. Chestnut-breasted Coronet

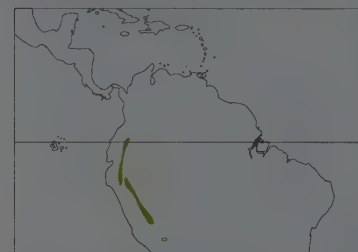
Boissonneaua matthewsii

French: Colibri de Matthews **German:** Rotbauchkolibri **Spanish:** Colibrí Pechirrojo

Taxonomy. *Trochilus Matthewsii* Bourcier, 1847, Peru.

Despite extensive range, species shows no marked geographical variation. Monotypic.

Distribution. Andes of extreme SE Colombia, Ecuador and Peru (on W slope S to Cajamarca, on E slope S to Cuzco).



Descriptive notes. 12 cm; 7.0-7.7 g. Sexes similar. Bill straight, thickish and black. Male shining metallic green above and chestnut-rufous below, with throat more or less spotted with green discs; tail only slightly forked, the central pair of rectrices bronze-green and remainder rufous with bronze-green edges and tips; sparsely developed tibial tufts light cinnamon in colour and rather inconspicuous. Immature with more extensive green areas on underparts, upperparts with cinnamon feather edges, especially on rump.

Habitat. Inhabits humid pre-montane forest in subtropical areas at elevations of 1200-

2600 m, occasionally up to 3000 m in Peru. Usually found inside forest, less often at edges or in more open vegetation.

Food and Feeding. Establishes territories around clusters of flowers and can be seen foraging for nectar mainly at canopy level. Often clings to flowers while feeding. Occasionally several individuals may gather at flowering trees. Additionally, feeds on insects obtained by hawking from high perches. Territorial and highly pugnacious like all members of genus. No further information.

Breeding. No data concerning season. The nest is cup-shaped and consists mainly of moss and lichen. Clutch size 2; incubation by female. First breeding in second year. No further information.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Fairly common. Range of present species coincides with the distribution of humid pre-montane forest; this is evident in W Peru, where species is restricted to the northern part of the Andes. Only a few records from Colombia. Has been recorded in North Podocarpus National Park (Ecuador).

Bibliography. Best *et al.* (1997), Brown & Bowers (1985), Butler (1979), Davies *et al.* (1994), Fjeldså & Krabbe (1990), Hilty & Brown (1986), Meyer de Schauensee (1982), Mobbs (1972b), Olog (1968), Parker *et al.* (1982), Renjifo *et al.* (1997), Salaman & Mazariegos (1998b), Stotz *et al.* (1996), Williams & Tobias (1994), Wittmann (1986), Zimmer (1951b).

201. Velvet-purple Coronet

Boissonneaua jardini

French: Colibri de Jardine **German:** Hyazinthkolibri **Spanish:** Colibrí Sietecolores
Other common names: Jardine's Hummingbird

Taxonomy. *Trochilus Jardini* Bourcier, 1851, Nanegal, Ecuador.

Monotypic.

Distribution. Pacific slope of W Andes in SW Colombia (Cerro Tatamá to Nariño) and NW Ecuador.



Descriptive notes. 11-12 cm; 8.0-8.5 g. Bill straight, black. Male shining bluish-green above with head and throat velvety black; crown, breast and belly glittering purplish-blue; underwing-coverts cinnamon and conspicuous in flight; tail slightly forked, central feathers black, the rest white with black tips and edges; small leg puffs also white. Female similar but duller in coloration, with feathers of breast and belly fringed buff; wings are shorter and tail less deeply forked than in male. Immature like female.

Habitat. Prefers wet mossy forests and forest borders in tropical and subtropical zones, but

can also be found at shrubby clearings in Pacific lowlands and on lower slopes. Records range from 350 to 2200 m, commonest above 1200 m.

Food and Feeding. Territorial, usually seen feeding at flowers from lower strata to tree tops. Insects are caught in the air by hawking. No further information.

Breeding. Jan-Mar. Nest cup-shaped, made of moss and lichen, placed on a horizontal branch or thin fork. Clutch size 2; incubation by female. First breeding in second year. No further information.

Movements. Sedentary, but seasonal altitudinal dispersal known in Colombia.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Chocó EBA. Uncommon and very local, most frequently found in the area around the type locality in NW Ecuador. Comparatively few Colombian records, mostly from S Nariño, where regularly recorded in protected areas, notably La Planada and Río Nambi Reserves.

Bibliography. Best *et al.* (1997), Brown & Bowers (1985), Butler (1979), Hilty & Brown (1986), Kirwan & Marlow (1996), Meyer de Schauensee (1949, 1982), Mobbs (1972b), Olog (1968), Ruschi (1961d, 1973b), Rutgers & Norris (1972), Salaman (1996), Salaman & Mazariegos (1998b), Stattersfield *et al.* (1998), Stotz *et al.* (1996).

Genus *AGLAEACTIS* Gould, 1848

202. Shining Sunbeam

Aglaeactis cupripennis

French: Colibrí étincelant **German:** Rostrotter Andenkolibri **Spanish:** Colibrí Cobrizo
Other common names: Copper-winged Hummingbird

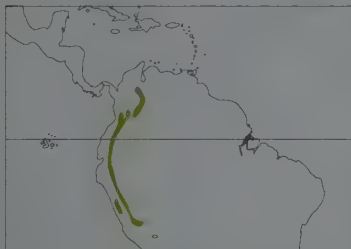
Taxonomy. *Trochilus cupripennis* Bourcier, 1843, Colombia.

Forms a superspecies with *A. castelnaudii* and possibly with *A. aliciae*. Although the morphological variation in the genus might suggest past gene flow between present species and *A. castelnaudii*, they are nowadays reproductively isolated in the zone of overlap. Occasionally considered to include *A. aliciae* as a race. Otherwise, up to six races of present species have been accepted at various times, with *aequatorialis* (N & C Ecuador), *parvulus* (S Ecuador, N Peru), *cajabambae* and *ruficauda* (both of NC Peru) replacing each other southwards through Ecuador and Peru, but morphometric and plumage characters strongly indicate clinal variation, and all four now subsumed into nominate. Two subspecies currently recognized.

Subspecies and Distribution.

A. c. cupripennis (Bourcier, 1843) - all three Andean ranges of Colombia, Ecuador and Peru (S to Huánuco and Lima).

A. c. caumatnotus Gould, 1848 - C & SC Peru (Junín, Apurímac, Cuzco).



Descriptive notes. 12-13 cm; male 7.6-8.1 g, female 6.9-7.5 g. Male has short, straight, black bill; crown and mantle dark brown, lower back to rump iridescent lilac-gold shading to shining silver-green on uppertail-coverts; throat rufous with dusky grey dots, light buff patches on breast, rufous brown on belly; rectrices range from dark brown to rufous, and are usually edged bronze. Female similar to male, often with iridescent lilac-golden and green on back reduced, sometimes absent. Immature light brown, lacks iridescent colours on back. Within nominate, clinal variation towards south shows increase in brightness of underparts.

darkness of crown, and amount of rufous in tail. Race *caumatnotus* iridescent amethyst on rump, uppertail-coverts purplish-amethyst.

Habitat. Sub-*páramo* to open *páramo* with scattered shrubs and trees, upper cloudforest, semi-arid montane ridges with interspersed trees at 2500-4300 m. Forages from lowest strata to tree tops.

Food and Feeding. Nectar of flowering terrestrial bromeliads, vines and trees, such as *Puya*, *Bomarea*, *Fuchsia*, *Centropogon*, *Embothrium*, *Mutisia*, *Passiflora* and *Tristerix*. Insects are caught in the air by hawking. Male defends feeding territories at nectar-rich flowering stands.

Breeding. All year round. Mar-Sept (Colombia), Feb-Apr (Ecuador), Nov, Apr (Peru). Cup-shaped compact nest of moss and cobweb, sometimes decorated with pieces of bark, leaf and lichen on outer wall, lined with soft white or brown plant fibre; built on branch or attached to epiphyte near tree tops, 4-10 m above the ground, occasionally up to 15 m. Clutch size 2; incubation 16-18 days, by female; chick black with some buff-coloured dorsal down; fledging at 24-27 days. First breeding in second year.

Movements. Altitudinal migrant in most parts of Colombia, descending seasonally to lower elevations.

Status and Conservation. Not globally threatened. CITES II. Generally fairly common; accepts a wide range of high Andean habitats including farmland with scattered stands of trees. Occurs in several protected areas throughout its range such as Puracé National Park (Colombia), and Las Cajas National Recreation Area and North Podocarpus National Park (Ecuador).

Bibliography. Berlepsch (1898), Best *et al.* (1997), Bloch *et al.* (1991), Butler (1979), Carriker (1933), Fjeldså (1995), Fjeldså & Krabbe (1990), Hilty & Brown (1986), Koepcke (1954, 1957, 1958, 1961, 1970), Krüger *et al.* (1982), Moynihan (1979), Parker & O'Neill (1980), Parker *et al.* (1982), Peters & Griswold (1943), Ruschi (1961c), Sanft (1970), Schuchmann (1985a), Schuchmann & Abersfelder (1986), Schuchmann *et al.* (1983), Stotz *et al.* (1996), Wiedenfeld (1985), Williams & Tobias (1994), Zimmer (1951b).

203. White-tufted Sunbeam

Aglaeactis castelnaudii

French: Colibri de Castelneau **German:** Rotbrust-Andenkoliбри **Spanish:** Colibri Condecorado

Taxonomy. *Trochilus Castelnaudii* Bourcier and Mulsant, 1848, mountains near Cuzco, Peru. Forms a superspecies with *A. cupripennis* and possibly with *A. aliciae*. May be sister-species of *A. pamela*. Although the morphological variation in the genus might suggest past gene flow between *A. cupripennis* and present species, they are nowadays reproductively isolated in the zone of overlap. Two subspecies recognized.

Subspecies and Distribution.

A. c. regalis Zimmer, 1951 - Andes of Huánuco, Pasco and Junín (C Peru).

A. c. castelnaudii Bourcier & Mulsant, 1848 - Andes of Huancavelica, Ayacucho, Apurímac and Cuzco (SC Peru).



Descriptive notes. 12 cm; 7.8-5 g. Bill straight, black. Immediate impression is fuscous with tawny tail, the shining back is displayed during hovering. Male above fuscous black with strong magenta reflection on rump and lower back; below dull brown with blackish upper throat and pectoral band and white feather tuft on central breast; tail forked. Female with less iridescent back and less fork in tail. Immature more uniform brown with no iridescent feathers. Race *regalis* has shorter bill; generally more rufous brown, with rufous tail.

Habitat. Inhabits patches of evergreen montane forest in slightly drier zones and often at much greater altitudes than *A. cupripennis*. Particularly common in *Escallonia* and *Polylepis* forests with abundant flowering vines. Subordinate to *A. cupripennis*, keeping low in the vegetation where the other species is present; at 3500-4300 m, rarely to 4600 m.

Food and Feeding. Takes nectar from flowers of *Barnadesia*, *Berberis*, *Brachyotum*, *Centropogon*, *Labiatae*, *Lupinus*, *Salpichroa* and *Siphocampylus*. Always feeds clinging to the flowers. Also takes insects in the air.

Breeding. Not known.

Movements. Remains in the same area during short periods of heavy snow. However, seasonal habitat shifts may take place in the dry season.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Peruvian High Andes EBA. Common at very few sites. Although its habitat has been destroyed in much of Huancavelica and Ayacucho, and in Cuzco species has become restricted to Cordilleras Vilcanota and Vilcabamba, many suitable patches of habitat remain in Apurímac. Occurs in the small Machu Picchu Historical Sanctuary.

Bibliography. Fjeldså (1991, 1992, 1995), Fjeldså & Kessler (1996), Fjeldså & Krabbe (1990), Meyer de Schauensee (1982), Morrison (1948), Parker *et al.* (1982), Schuchmann (1985a), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Zimmer (1930, 1951b).

204. Purple-backed Sunbeam

Aglaeactis aliciae

French: Colibri d'Alice **German:** Weißbrust-Andenkoliбри **Spanish:** Colibri de Alicia

Taxonomy. *Aglaeactis aliciae* Salvin, 1896, Succa, 10,000 feet [c. 3000 m], La Libertad, north Peru. May belong to the superspecies of *A. cupripennis* and *A. castelnaudii*. Taxonomic status still unresolved: some authors consider it a race of *A. cupripennis*, since immature birds have a buff-spotted chin and throat turning pure white after the first moult; otherwise, it resembles race *caumatnotus* of that species. Monotypic.

Distribution. E slope of W Andes at Succa, La Libertad (N Peru).



Descriptive notes. 12-13 cm; 7.3-8.3 g. Male has short, straight, black bill; head and mantle earth brown, lower back and rump iridescent amethyst becoming golden green on uppertail-coverts; lores, chin, throat, central breast and pectoral tufts white, otherwise darkish brown; rectrices bronze, white at base. Female similar to male but iridescent parts on back reduced to uppertail-coverts or completely lacking. Immature similar to adult female but with buffy spots on lores, chin, throat and central belly; throat may even be completely buff-coloured; head feathers fringed buff.

Habitat. Semi-open Andean slopes with *Alnus*

trees and shrubs at 3000-3200 m.

Food and Feeding. Nectar of flowering mistletoe *Tristerix longibracteatum* and small insects. Food spectrum and foraging behaviour are little known.

Breeding. No data available. Season may be around Sept-Aug; males with slightly enlarged testes recorded in Jun.

Movements. Sedentary.

Status and Conservation. VULNERABLE. CITES II. Restricted-range species: present in Marañón Valley EBA. Classified as a threatened species on the basis of restricted range and limited information available regarding current condition of habitat. May tolerate some degree of habitat change, like congeners.

Bibliography. Carriker (1933), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Fjeldså & Krabbe (1990), Olrog (1968), Parker *et al.* (1982), Schuchmann (1985a), Stattersfield *et al.* (1998), Stephens & Traylor (1983), Stotz *et al.* (1996), Wege & Long (1995), Zimmer (1951b).

205. Black-hooded Sunbeam

Aglaeactis pamela

French: Colibri paméla **German:** Schwarzbauch-Andenkoliбри **Spanish:** Colibri Negroito

Taxonomy. *Ornismya Pamela* d'Orbigny, 1838, Yungas of Bolivia.

May be sister-species of *A. castelnaudii*. Monotypic.

Distribution. Cordillera Real of Bolivia.



Descriptive notes. 13 cm; 7.8-5 g. Bill short, straight, black. Generally black with contrasting white pectoral tuft. Male has shining bluish-malachite rump (sometimes spreading over most of the back); tail slightly forked, rufous. Female duller black than male, less iridescent on back and with tail less forked. Immature resembles adult female.

Habitat. Most common in tree-line shrubbery in the transition zone between humid slopes and montane basins, especially in rather open areas with some *Barnadesia* and *Polylepis* patches, at 3000-3500 m or rarely down to 1800 m. Also in humid upper montane forest.

Food and Feeding. Forages for nectar at *Barnadesia* and *Berberis* bushes, *Puya* and *Centropogon*. Always feeds clinging to the flowers. Also takes insects.

Breeding. Probably Sept-Mar, but no nests recorded. Evidently first breeds in second year.

Movements. Some records at low elevations suggest that there is some local altitudinal migration.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Bolivian and Peruvian Upper Yungas EBA. Common in Yungas of La Paz and Cochabamba; also elsewhere, even in places with considerable man-induced habitat fragmentation. Protected in the Carrasco-Ichilo and Amoro National Parks.

Bibliography. Bond & Meyer de Schauensee (1943), Fjeldså (1992, 1995), Fjeldså & Kessler (1996), Fjeldså & Krabbe (1990), Meyer de Schauensee (1982), Niethammer (1953), Olrog (1968), Remsen & Traylor (1989), Rentinck (1981), Schuchmann (1985a), Stattersfield *et al.* (1998), Stotz *et al.* (1996).



Genus *OREOTROCHILUS* Gould, 1847

206. Andean Hillstar

Oreotrochilus estella

French: Colibri estelle **German:** Estella-Andenkolibri **Spanish:** Colibrí Puneño
Other common names: Stripe-bellied Hillstar (*estella*); Bolivian Hillstar (*bolivianus*)

Taxonomy. *Trochilus Estella* d'Orbigny and Lafresnaye, 1838, La Paz and Potosí, Bolivia. Forms a superspecies with *O. chimborazo*, *O. stolzmanni* and *O. leucopleurus*, and all four have been considered conspecific, but separated largely on morphological grounds; the last-mentioned overlaps slightly with present species, and some hybridization reported, but despite this it is the form least frequently lumped into present species; *O. stolzmanni* frequently considered a race of present species. Two subspecies recognized.

Subspecies and Distribution.

O. e. estella (d'Orbigny & Lafresnaye, 1838) - Andes of SW Peru, W Bolivia, N Chile and NW Argentina.

O. e. bolivianus Boucard, 1893 - Andes of C Bolivia (Cochabamba).



Descriptive notes. 13-15 cm; male c. 8-8 g, female c. 8-0 g. Male has medium-sized, slightly decurved black bill; drab brown above; very shiny emerald green gorget with black border, mostly white below with rufous median line on belly; tail forked, white, central feather pair and outer edge and tip of lateral feathers bronzy-black. Female drabber below, with finely speckled throat, tail greenish-black, outer 3-4 feathers with white inner webs at base and tip. Immature more greyish, with yellow base to mandible, immature male with dark glaucous gorget. Male of race *bolivianus* has median line on belly chestnut spotted black.

Habitat. Inhabits *puna* grasslands, where most commonly found around rocky outcrops and in other places with a variety of flowering shrubs. Often particularly common near houses, in stands of *Puya raimondii* and at edges of *Polylepis* woodlands. In the breeding season the sexes segregate to different habitats, where females hold territories in bushy gorges near rocks, while males are territorial and wander through the open grassland. Roosts (in torpor) clinging to vertical rock surface, selecting well protected sites in caves and deep crevices during the southern winter. Occurs from 2400 m to 5000 m, commonest at 3500-4500 m.

Food and Feeding. Feeds while perched, taking nectar from the orange flowers of *Chuquiraga spinosa* shrubs and from low cushion cacti. Also visits other flowering shrubs such as *Barnadesia*, *Berberis*, *Buddleia*, *Malva* and *Ribes*, *Bomarea* vines, *Puya* and flowering *Eucalyptus* trees. In the rainy season visits a variety of mainly red flowers more or less hidden in the grassland, such as *Cajophora*, *Centropogon*, or cushion-like cacti. Gleans arthropods from vegetation and sometimes catches insects high up in the air.

Breeding. Sept-Dec. Females hold territories in bushy gorges with rocks, several females nesting semi-colonially in particularly suitable places. Occasionally places nest under the "skirt" of a *Puya raimondii*. Large woolly cup-nest is glued to rock surface. Clutch size 2; incubation 20 days; fledging period 38 days though shorter in warm places; possibly sometimes lays second clutch. Nesting success 68%, which is exceptionally high for a hummingbird. Probably first breeds in second year.

Movements. During the breeding season males move around in the grassland. Remains in the uplands during short periods of snow, but may disperse to adjacent warmer valleys during the southern winter.

Status and Conservation. Not globally threatened, CITES II. One of the commonest *puna* birds, except in areas where traditional burning and overgrazing have severely reduced plant diversity. Protected in several areas, notably Calipuy National Sanctuary, Huascarán National Park and Salinas y Aguada Blanca National Reserves (Peru), Ulla-Ulla and Sajama National Parks (Bolivia) and Lauca National Park (Chile).

Bibliography. Araya & Chester (1993), Bond & Meyer de Schauensee (1943), Canevari *et al.* (1991), Carpenter (1974, 1976), Dorst (1956, 1962), Fjeldså (1983, 1992), Fjeldså & Kessler (1996), Fjeldså & Krabbe (1990), Fjeldså & Mayer (1996), Flores & Capriles (1998), Johnson (1967, 1972), Koepeke (1970), Langner (1973), Niethammer (1953), Parker *et al.* (1982), Pearson (1953), de la Peña (1994), Remsen & Traylor (1989), Rocha & Peñaranda (1995), Rocha & Quiroga (1996), Rutgers & Norris (1972), Stotz *et al.* (1996), Vuilleumier & Simberloff (1980), Zimmer (1930, 1951a).

207. Ecuadorian Hillstar

Oreotrochilus chimborazo

French: Colibri du Chimborazo **Spanish:** Colibrí del Chimborazo
German: Ecuador-Andenkolibri
Other common names: Violet-hooded Hillstar; Chimborazo Hillstar (*chimborazo*)

Taxonomy. *Trochilus Chimborazo* DeLattre and Bourcier, 1846, Mount Chimborazo, Ecuador. Forms a superspecies with *O. estella*, *O. stolzmanni* and *O. leucopleurus*, and all four have been considered conspecific, but separated largely on morphological grounds. Race *soederstroemi* is sometimes thought to be an intergrade of *jamesonii* and nominate, but it is apparently isolated geographically from both of them. Three subspecies currently recognized.

Subspecies and Distribution.

O. c. jamesonii Jardine, 1849 - mountains of extreme S Colombia and N Ecuador (Cotacachi, Pichincha, Iliniza, Antisana, Cotopaxi).

O. c. soederstroemi Lönnberg & Rendahl, 1922 - C Ecuador (Mt Quilotoa).

O. c. chimborazo (DeLattre & Bourcier, 1846) - C Ecuador (Mt Chimborazo, possibly also Azuay).



Descriptive notes. 13 cm; 7-8-8-1 g. Bill black, slightly curved. Male upperparts dark olive green; entire head and upper throat covered by a glittering purplish-blue hood, lower throat glittering green, bordered below by a narrow black breast band; rest of underparts white with dark undertail-coverts and thin dark line down centre of belly; tail only slightly forked, central tail feathers dark, remainder white with dark tips and edges, the outermost pair largely dark and with the outer web narrower. Female pale bronze-green above, tail dark shining green, less forked than in male, the outer pair of rectrices white at base and tip; throat whitish, densely speckled with brown discs, rest of underparts pale greyish. Immature resembles female, but juvenile male can be recognized by pale region across upper breast; immature male has dark glaucous hood. Northernmost race *jamesonii* has an entirely violet hood, and outer rectrices show less white than in nominate; race *soederstroemi* has only a few green feathers at lower border of throat patch.

Habitat. Inhabits highest vegetated zones up to snow-line at elevations of 3500-5200 m. This high-altitude habitat is split into a series of "islands" along a number of isolated volcanic mountains. The species is typically found near upper border of *páramo* zone, mainly in rather arid *puna*-like grassland habitats, sometimes with some stunted trees and shrubs, but also on more humid *páramo* and on rocky slopes. Especially near secluded ravines, but also uses man-made habitats resulting from frequent burning of vegetation and pastures. At night roosts in caves and crevices, mostly in a torpid state to cope with low night temperatures. Also uses caves for shelter during the hailstorms frequent in this high-altitude habitat.

Food and Feeding. Territorial and notably aggressive. Often perches conspicuously on top of a shrub for long periods, but uses lower and more protected perches in windy weather. While feeding, typically clings to flowers with its comparatively large feet rather than hovering. The most important nectar source is *Chuquiraga insignis*, a composite scrub with orange flowers. Among other food plants recorded are Malvaceae and *Puya*. This diet is supplemented by a considerable number of insects, obtained mainly by hawking but also by gleaning from leaves and cliff surface.

Breeding. Mainly Oct-Feb (*jamesonii*), but nests found throughout the year. The nest consists of moss, roots, dry grass, feathers, rabbit fur and plant down and is very large in order to protect against severe weather and cold, especially at night; typically situated in cave, gully, or wall of steep ravine, usually below an overhang for additional protection; where such places are scarce several nests often found in close vicinity. Nest may also be built in a *Polylepis* tree or suspended from small ferns. Shape varies depending on substrate to which nest is attached: nest-sites usually 0-6-6 m above ground. Clutch size 2; incubation by female; incubation and fledging periods very long; exact figures lacking, but probably as in *O. estella*. Chick black and naked; young birds continue to use the nest for some time after they can fly.

Movements. Some altitudinal movements have been observed, possibly as an adaptation to the harsh highland climate.

Status and Conservation. Not globally threatened, CITES II. Fairly common; typical habitat is not subject to a high level of degradation, and species also accepts man-made environments. Occurs in several protected areas, e.g. Cotopaxi National Park and Las Cajas National Recreation Area (Ecuador).

Bibliography. Berlioz (1933b, 1971b, 1974), Berlioz & Jouanin (1942), Best *et al.* (1997), Butler (1979), Chapman (1926), Fjeldså & Krabbe (1990), French & Hodges (1959), Hilty (1994), Meyer de Schauensee (1982), Olrog (1968), Ortiz & Bleiweiss (1982), Ortiz & Carrión (1991), Rothschild (1927), Ruschi (1949b), Salaman & Gandy (1994), Salaman & Mazariegos (1998b), Smith (1969), Stotz *et al.* (1996), Vuilleumier (1976), Woods *et al.* (1998), Zimmer (1951a).

208. Green-headed Hillstar

Oreotrochilus stolzmanni

French: Colibri de Stolzmann **German:** Grünkopf-Andenkolibri **Spanish:** Colibrí de Stolzmann
Other common names: Stolzmann's Hillstar

Taxonomy. *Oreotrochilus stolzmanni* Salvin, 1895, Huamachuco and near Cajamarca, Peru. Forms a superspecies with *O. estella*, *O. chimborazo* and *O. leucopleurus*, and all four have been considered conspecific, but separated largely on morphological grounds; present species frequently lumped into *O. estella*. Monotypic.

Distribution. Andes of N & C Peru (Cajamarca, Huánuco); recently reported from S Ecuador.



Descriptive notes. 13-14 cm; 7-9-8-4 g. Male has medium-sized, slightly decurved black bill; upperparts greenish with bronzy sheen; throat emerald green, black line separating throat from white underparts; fine black line along central belly; tail whitish, central rectrices dull bronzy. Female similar to male, below pale white, greyish spots on throat, tail greenish-black, outer rectrices with white inner webs at base and tip. Immature similar to adult female.

Habitat. Rocky alpine grassland of the Altiplano (*puna*) with scattered stands of *Puya* and *Polylepis* forest, at 3600-4200 m. Forages below 3 m; usually perches, rather exposed,

on *Puya* inflorescences or rocks, sometimes on the ground, in open terrain. At night, birds seek shelter in rocky cavities or in caves, where several birds often roost closely together, clinging to the rocky wall.

Food and Feeding. Primarily nectar and pollen of flowering *Chuquiraga*, *Cajophora*, *Puya* and cacti. Usually perches on or clings to flowers while feeding. Insects are caught in the air by hawking. Males and to a lesser extent females defend feeding territories against intruders.

Breeding. Feb-Jun, sometimes up to Aug. Bulky cup-shaped nest of moss and soft plant fibres is built in rock cavities close under overhangs, roofs of houses, or even inside open buildings like

barns. Clutch size 2; incubation 19-21 days, by female; chick darkish with two dorsal rows of dull grey down; fledging period 36-40 days. First breeding in second year.

Movements. Mostly sedentary, with seasonal local wandering to lower elevations.

Status and Conservation. Not globally threatened, CITES II. Locally common, especially on alpine meadows with mats of *Chusquea*. The habitat of this species being mostly unsuitable for agricultural purposes, it would appear that no immediate conservation measures are required.

Bibliography. Berlioz & Jouanin (1942), Best *et al.* (1997), Fjeldså & Krabbe (1990), Olrog (1968), Rousseau-Decelle (1942), Sanft (1970), Simon & Hellmayr (1908), Zimmer (1951a).

209. White-sided Hillstar

Oreotrochilus leucopleurus

French: Colibri à flancs blancs

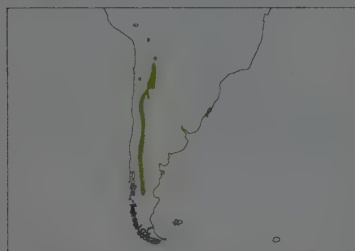
Spanish: Colibrí Cordillerano

German: Weißflanken-Andenkolibri

Taxonomy. *Oreotrochilus leucopleurus* Gould, 1847, Chilean Cordilleras.

Forms a superspecies with *O. estella*, *O. chimborazo* and *O. stolzmanni*, and all four have been considered conspecific, but separated largely on morphological grounds; *O. estella* overlaps slightly with present species, and some hybridization reported, in spite of which present species is the form least frequently lumped into *O. estella*. Monotypic.

Distribution. S Bolivia (Tarija) S through Andes to SC Chile (Bío-Bío) and S Argentina (WC Santa Cruz).



Descriptive notes. 13-15 cm (bill 2 cm), 7.9-8.4. Bill slightly curved, black. Resembles *O. estella*, but male has broad blue-black median stripe below, and tail more rounded because of shorter, narrower and inwards-curving outer rectrices, which are white only at base. Female and juvenile have narrow outer rectrices with complete dark transverse bar.

Habitat. Puna with dwarf bushes, columnar cacti and Puya, at 1200-4000 m, sometimes even to the snow-line.

Food and Feeding. Probably as *O. estella*; feeds on nectar from flowers of *Barnadesia*, *Berberis* and *Chusquea* bushes, larger Puya

species and probably some herbs.

Breeding. Nov-Dec. Large cup-shaped nest is glued to a vertical rock-face, usually in a well protected site. Clutch size 2. No further information.

Movements. During the southern winter normally leaves its Chilean territory, but a record in Jul at 600 m in N Chile demonstrates altitudinal displacements within Chile.

Status and Conservation. Not globally threatened, CITES II. Generally common; limits of range in Argentina recently found to extend much further S than previously thought. Large tracts of core habitat are under slight pressure from man, including several protected areas of considerable extent, such as Laguna de Los Pozuelos, Olaroz-Cauchari, Laguna Brava, San Guillermo, Volcán Tupungato and Lanín (Argentina); also present in Cerro La Campana National Park (Chile).

Bibliography. Araya & Chester (1993), Bond & Meyer de Schauensee (1943), Canevari *et al.* (1991), Carpenter (1976), Fjeldså & Krabbe (1990), Johnson (1967), Marín *et al.* (1989), Narosky & Yzurieta (1993), Navas (1968), Olrog (1968, 1984), de la Peña (1994), Remsen & Traylor (1989), Stotz *et al.* (1996), Wetmore (1926).

210. Black-breasted Hillstar

Oreotrochilus melanogaster

French: Colibri à plastron noir

Spanish: Colibrí Pechinegro

German: Schwarzbrust-Andenkolibri

Taxonomy. *Oreotrochilus melanogaster* Gould, 1847, no locality = Maraynioc, Junín, Peru.

On present knowledge, it is not fully clear whether this is a melanistic representative of the *O. estella* superspecies or an independent species. Monotypic.

Distribution. C Peru, in Junín and Huancavelica and locally into adjacent mountains of Ancash, Lima, Pasco and Ayacucho.



Descriptive notes. 13-14 cm; c. 8.4 g. Bill slightly decurved, black. Male darker and more bronzed above than *O. estella*; gorget shining emerald green, rest of underparts black, flanks drab greyish-brown; tail slightly forked, blue-black. Female like that of *O. estella* but lacks white at base of tail feathers.

Habitat. Puna slopes, usually with a high density of *Chusquea spinosa* bushes and low cushion cacti, and with some rocky areas usually with rich herbaceous vegetation in sheltered recesses. Often in gardens, and also recorded in a stand of *Puya raimondii* at 3500-4400 m.

Food and Feeding. In Junín feeds most of the year mainly from the flowers of *Chusquea spinosa* shrubs, but in the puna of Huancavelica exploits cactus flowers. Opportunistically trap-lines, searching for red flowers of *Cajophora*, *Castilleja* and *Puya*, and occasionally visits flowering *Cassia* and *Eucalyptus*. Hawks for insects high up in the air.

Breeding. Feb-Mar. Nests in sheltered places on rocks and under edge of farmhouse roofs. Large cup-shaped nest glued to the substrate. Clutch size 2. Probably first breeds in second year. No further information.

Movements. Although the species stays all year on the Junín Altiplano, it has been suggested that it leaves the puna in Huancavelica when cacti are not flowering.

Status and Conservation. Not globally threatened, CITES II. Restricted-range species: present in Junín Puna EBA. Generally fairly common, and abundant in hills around L. Junín, inside Junín and Huayllay National Reserves, and at many sites in Huancavelica. The puna slope habitat is not under particular threat in this region.

Bibliography. Carpenter (1976), Fjeldså (1983, 1992), Fjeldså & Kessler (1996), Fjeldså & Krabbe (1990), Koepeke (1970), Meyer de Schauensee (1982), Morrison (1939), Olrog (1968), Parker *et al.* (1982), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Zimmer (1951a).

211. Wedge-tailed Hillstar

Oreotrochilus adela

French: Colibri adèle

German: Rotflanken-Andenkolibri

Spanish: Colibrí de Cochabamba

Taxonomy. *Trochilus Adela* d'Orbigny and Lafresnaye, 1838, Chuquisaca, Bolivia.

Monotypic.

Distribution. Montane basins and pre-puna of S Bolivia (S La Paz to Potosí and Chuquisaca); also reported from Cota-cota (N La Paz).



Descriptive notes. 11-13 cm; 7.4-8.3 g. Bill slightly decurved, black. Upperparts grey-brown, faintly bronzed. Male with gorget glittering vivid green, underparts chestnut with bold black central area; tail blue-black with cinnamon inner webs of all except central feathers. Female has throat white with greyish and green spots, below pale rufous; tail with white feather tips. Immature resembles adult female.

Habitat. Mainly in semi-arid to temporarily humid areas at 2600-4000 m with dispersed mesophytic shrubs; often in gullies with *Polylepis* trees with many parasitic loranthaceans (*Tristerix*) and *Barnadesia* thickets. May even be found in degraded habitats with *Dodonaea* bushes, provided that scattered columnar cacti and some taller bushes are present.

Food and Feeding. Forages for nectar at flowers of *Barnadesia*, *Mutisia*, Lorantheaceae mistletoes, *Puya* and columnar cacti. Also takes some insects.

Breeding. Eggs reported from Nov, juveniles from Feb and Jun. Large cup-nest glued to rock surface. No further information.

Movements. Probably some individual dispersal or local movements, but not well known.

Status and Conservation. Not globally threatened, CITES II. Currently considered Near-threatened. Restricted-range species: present in High Andes of Bolivia and Argentina EBA. Generally rather uncommon, but apparently able to survive in areas that are severely degraded by burning and overgrazing, as long as some bushy patches remain in ravines. Because of the dense human population in its range, adequate protected areas need to be established in order to cover core habitat for this species.

Bibliography. Álvarez & Blendinger (1995), Barnett *et al.* (1998), Bond & Meyer de Schauensee (1943), Carpenter (1976), Fjeldså (1992), Fjeldså & Kessler (1996), Fjeldså & Krabbe (1990), Meyer de Schauensee (1982), Olrog (1968), Remsen & Traylor (1989), Sagot (1998a), Schmitt *et al.* (1997), Stattersfield *et al.* (1998), Stotz *et al.* (1996).

Genus LAFRESNAYA Bonaparte, 1850

212. Mountain Velvetbreast

Lafresnaya lafresnayi

French: Colibri de Lafresnaye

German: Samtbauchkolibri

Spanish: Colibrí Aterciopelado

Other common names: Velvetbreast

Taxonomy. *Trochilus La Fresnaye*, Boissonneau, 1840, Bogotá, Colombia.

Genus apparently close to *Oreotrochilus*, based on behaviour and external morphology. Population from Páramo de Tamá (extreme W Venezuela) often separated as race *tamae*; another in N Peru as race *orestes*, but probably better considered synonymous with *rectirostris*. "*Coeligena lawrencei*" is probably a hybrid of present species and *Coeligena torquata*. Five subspecies recognized.

Subspecies and Distribution.

L. l. liriopae Bangs, 1910 - Santa Marta Mts (NE Colombia).

L. l. greenewalti Phelps & Phelps, Jr., 1961 - W Venezuela (NE Táchira, Mérida, S Trujillo).

L. l. lafresnayi (Boissonneau, 1840) - extreme W Venezuela (Páramo de Tamá in S Táchira) and E & C Andes of Colombia.

L. l. saul (DeLatre & Bourcier, 1846) - Andes of SW Colombia, Ecuador and N Peru.

L. l. rectirostris Berlepsch & Stolzmann, 1902 - N & C Peru.



Descriptive notes. 11.5-12 cm (including bill of 3 cm); 4.5-6.3 g. Male has long, thin, decurved black bill; upperparts grass green; white postocular spot, throat and breast iridescent emerald green, belly velvet black, central rectrices bronze-green, rest buff (nominate race) or whitish (all other races), tipped black. Female similar to male but with underparts buff (nominate race) or white (all other races) with iridescent green discs. Immature similar to female but head feathers have brownish fringes; immature male separable from immature female by black belly, but otherwise similar. Race *liriopae* similar to nominate but central

pair of tail feathers coppery green, contrasting with the back; *greenewalti* paler and more yellowish-green overall; *saul* has outer rectrices pure white, tipped greenish-bronze; *rectirostris* has broad black band on tips of rectrices.

Habitat. Borders of humid montane forest and shrubby slopes from 1900 to 3400 m. Less common inside the forest. Forages at low levels, 0.5-3 m. Most numerous at 2000-2800 m.

Food and Feeding. Nectar of flowering *Centropogon*, *Castilleja*, *Siphocampylus*, *Salvia*, Lorantheaceae, Ericaceae and Gesneriaceae. Male occupies nectar-rich territories, female trap-lines between dispersed flower stands. Arthropods are caught in the air by hawking or gleaned from plant surfaces.

Breeding. Apparently during most of the year; Santa Marta, N Colombia, Jan-Mar; C Andes, S Colombia, Jul-Sept; W Colombia, Sept; NE Ecuador, Jan-Feb. Bulky cup-shaped nest of moss,

lichen and cobweb is built in vegetation covering steep rocks or roadbanks, sometimes on tree trunks at c. 1-3 m above ground. Clutch size 2; incubation 16-19 days, by female; chick darkish with sparse grey dorsal down; fledging period 23-26 days.

Movements. Marked seasonal movements to higher altitudes, in sub-*páramo* and *páramo*.

Status and Conservation. Not globally threatened. CITES II. Common in the Santa Marta Mts; in the Andes less numerous and patchily distributed. In Ecuador, occurs in several protected areas

such as Paschoa Forest Reserve, Las Cajas National Recreation Area and North Podocarpus National Park.

Bibliography. Baez *et al.* (1997), Berlioz (1932d), Best *et al.* (1997), Bloch *et al.* (1991), Butler (1979), Fjeldså & Krabbe (1990), Hilty & Brown (1986), Meyer de Schauensee & Phelps (1978), Parker *et al.* (1982), Phelps & Phelps (1961), Snow & Snow (1980), Stotz *et al.* (1996), Vélez & Velázquez (1998), Williams & Tobias (1994), Zimmer (1930, 1951b).

inches 3
cm 8



Genus *COELIGENA* Lesson, 1832

213. Bronzy Inca

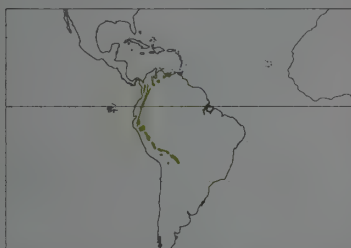
Coeligena coeligena

French: Inca céleste **German:** Bronzeandenkolibri **Spanish:** Inca Bronceado

Taxonomy. *Ornismya coeligena* Lesson, 1832. Mexico; error = Venezuela. Proposed race *zuloagae*, known only from type specimen from Falcón (NW Venezuela), probably represents individual variation of nominate; more study required. "*C. purpurea*", from Popayán (SC Colombia), may be hybrid of present species and *C. prunellei*; alternatively, might be a dark variety of *C. wilsoni*. Six subspecies recognized.

Subspecies and Distribution.

C. c. coeligena (Lesson, 1832) - N Venezuela (Lara E to Miranda).
C. c. zuliana Phelps & Phelps, Jr., 1953 - Sierra de Perijá, on Venezuela-Colombia border.
C. c. columbiana (Elliott, 1876) - Andes of NW Venezuela (Barinas, Lara, Táchira) and E & C Andes of Colombia.
C. c. ferruginea (Chapman, 1917) - C & W Andes of Colombia.
C. c. obscura (Berlepsch & Stolzmann, 1902) - Andes of extreme S Colombia, Ecuador and Peru.
C. c. boliviana (Gould, 1861) - Andes of C & SE Bolivia.



Descriptive notes. c. 14 cm; male c. 7.3 g, female c. 6.2 g. Male has long, straight, black bill, lower mandible often yellowish at base, head and upperparts dark bronzy-brown with distinct maroon sheen, becoming greenish on lower back; postocular spot white; throat and chest spotted white and streaked dusky grey, rest of underparts rufous brown, undertail-coverts rufous, edged cinnamon; tail forked, bronze. Female similar to male but has longer bill; tail less forked. Immature resembles adult female. Race *zuliana* has slightly more greenish plumage, less bronzy crown and upperparts; *columbiana* is smallest of all races, plumage

generally more olive; *ferruginea* similar to nominate but with throat less extensively white, and underparts more strongly washed tawny; *obscura* has darkest plumage, back more blackish, throat more greyish than white, large dark speckles; *boliviana* similar to nominate but discs on crown are dark green, tail bronzy blackish-purple, darker than in all other races.

Habitat. Edges of humid pre-montane forest, at 1500-2600 m. Sometimes in open terrain with scattered trees and in coffee plantations. Forages at periphery of vegetation.

Food and Feeding. Nectar of flowering *Fuchsia*, *Bomarea*, *Cavendishia*, *Centropogon*, *Heliconia* and *Siphocampylus*. Arthropods are caught by hawking and hover-gleaning. Feeds by trap-lining in lower to middle strata within and at edge of forest. Seldom seen in canopy of flowering trees where occasionally defends feeding territories.

Breeding. Nov-Mar. Nest cup-shaped, in understorey 1-1.5 m above ground, well hidden in fork of shrub, built of moss and plant fibres. Clutch size 2; incubation 15-16 days, by female; chick blackish with two dorsal rows of buffy down; fledging at 22-24 days.

Movements. Seasonal movements occur but not well understood, perhaps follows breeding season.

Status and Conservation. Not globally threatened. CITES II. Locally common. Although original habitat suffers from deforestation, species is not seriously affected because it accepts man-made habitats, like coffee plantations and similarly disturbed areas. Range includes several protected areas such as Henri Pittier National Park (Venezuela) and Cueva de los Guácharos National Park (Colombia). Imports for wild-bird trade in Europe during recent decades had no significant negative effect on populations.

Bibliography. Best *et al.* (1997), Bond & Meyer de Schauensee (1943), Butler (1979), Chapman (1917), Davies *et al.* (1994), Fjeldsá & Krabbe (1989, 1990), Hilty & Brown (1986), Meyer de Schauensee & Phelps (1978), Miller (1963), Olivares (1969), Olrog (1963c), Parker *et al.* (1982), Phelps & Phelps (1953), Remsen & Traylor (1989), Ridgely & Gaulin (1980), Schuchmann (1975b, 1978b, 1980d, 1989), Stotz *et al.* (1996), Zimmer (1951a).

214. Brown Inca

Coeligena wilsoni

French: Inca brun **German:** Brauner Andenkolibri **Spanish:** Inca Pardo

Taxonomy. *Trochilus Wilsoni* DeLatre and Bourcier, 1846. Juntas near Buenaventura, Colombia. Relationships uncertain within the complex containing present species, *C. prunellei*, *C. torquata* and *C. inca*; further studies needed. Forms a superspecies with *C. prunellei*. "*C. purpurea*", from Popayán (SC Colombia), might be a dark variety of present species; alternatively, may be hybrid *C. coeligena* x *C. prunellei*. Monotypic.

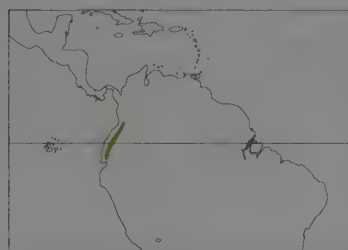
Distribution. Pacific slope of Andes of W & SW Colombia to W Ecuador.

Descriptive notes. c. 11-13 cm; male c. 6.9 g, female c. 6.5 g. Male has long, straight, black bill; upperparts reddish-bronze, similar to *C. coeligena*, becoming more greenish-olive especially on lower back; white postocular spot; underparts dull brown, amethyst throat patch, white patch on each side of breast; tail bronzy, forked. Female similar to male but has longer bill and smaller throat patch, tail less forked. Immature resembles female.

Habitat. Humid montane cloudforest at elevations of 700-1900 m, occasionally up to 2400 m.

Food and Feeding. Feeds on nectar of flowering epiphytic Ericads such as *Psammisia*, *Satyria*, *Macleania* and *Cavendishia*, vines and *Fuchsia*. Arthropods are usually caught by gleaning from vegetation, occasionally by hawking. Feeds by trap-lining, in lower levels within thick undergrowth.

Breeding. Jan-Jun. Cup-shaped nest of moss and soft seed fibre is built in fork of young tree, 2-3 m above ground. Clutch size 2; incubation 15-16 days, by female; chick black with two dorsal rows of buffy down; fledging at 22-26 days.



Movements. Seasonal short-distance movements probably following flowering of plants; no further data available.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Chocó EBA. Uncommon to locally common. Natural habitat under threat of deforestation; no precise information available as to whether or not this species accepts man-made habitats or even lightly disturbed areas. In Colombia, present in several protected areas, e.g. La Planada and Río Nambi Reserves. Has been imported to Europe on regular basis during recent decades.

Bibliography. Best *et al.* (1997), Butler (1979), Hilty (1997), Hilty & Brown (1986), Kirwan & Marlow (1996), Meyer de Schauensee (1982), Olrog (1968), Rutgers & Norris (1972), Salaman (1996), Salaman & Mazariegos (1998b), Schuchmann (1980d), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Williams & Tobias (1994).

215. Black Inca

Coeligena prunellei

French: Inca noir **German:** Blauschulter-Andenkolibri **Spanish:** Inca Negro

Taxonomy. *Trochilus Prunellei* Bourcier, 1843. Facativa, Colombia.

Relationships uncertain within the complex containing *C. wilsoni*, present species, *C. torquata* and *C. inca*; further studies needed. Forms a superspecies with *C. wilsoni*. Taxonomic status of "*C. assimilis*" uncertain: could represent a valid race of present species or a variation; further study required. "*C. purpurea*", from Popayán (SC Colombia), may be hybrid of present species and *C. coeligena*; alternatively, might be a dark variety of *C. wilsoni*. Monotypic.

Distribution. NC Colombia on W slope of C Andes (Quindío) and in E Andes (SE Santander, W Boyacá, W Cundinamarca).



Descriptive notes. c. 13.5 cm; 6.6-7 g. Male has long, straight, black bill, legs pale flesh-coloured; almost entire plumage purplish-black; throat patch small, greenish-blue; broken collar white, on both sides of breast; shoulders metallic blue; postocular spot white; undertail-coverts edged white, tail forked, black. Female similar to male, but has longer bill and less extensive blue on shoulders. Immature resembles female but lacks blue throat patch.

Habitat. Humid montane forest, primarily oak forest (*Quercus humboldtii*, *Trigonobalanus excelsa*) at 1000-2800 m; sometimes occurs in open country and along rivers in gallery forest.

Food and Feeding. Feeds on nectar of mainly pendent flowers with long corollas like *Aetanthus*, *Aphelandra*, *Burmeistera globosa*, *Fuchsia*, *Huileaea macrocarpa*, *Macrocarpaea*, *Palicourea demissa*, *P. vagans*, *Posoqueria*, *Psammisia falcata*, *Tilandsia turneri* and *Thibaudia rigidiflora*. Gleans and hawks for arthropods. Feeds by trap-lining from lower middle strata to canopy; lower in disturbed areas like clearings, parks and forest edge. Dominates other hummingbirds such as *Boissonneaua* or *Doryfera* at flowers, but rarely defends feeding territories.

Breeding. Probably May-Oct, based on gonadal condition. No further data available, nest undescribed.

Movements. No information available.

Status and Conservation. VULNERABLE. CITES II. Restricted-range species; present in Colombian East Andes EBA. Rare to locally fairly common. Recent records near Virolin indicate that it is common in this area; also in Cerro Carare (Boyacá), and the same holds for regular records around Laguna de Pedropalo. Major threats are destruction of humid oak forest, the main habitat, and also forest fragmentation. Although individuals are observed in relict forest patches, species is most numerous in more continuous areas of forest; accepts man-made habitats to some extent. Remaining forests are surrounded by intensive crop cultivation. The newly created Cachalú Biological Preserve, containing undisturbed *Quercus humboldtii* forest and sub-Andean rainforest, is partly aimed at offering this species additional protection.

Bibliography. Andrade & Repizzo (1994), Brooke (1988), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Fjeldsá & Krabbe (1990), Hilty (1985), Hilty & Brown (1986), King (1978/79), Meyer de Schauensee (1949), Olivares (1969), Paynter & Traylor (1981), Renjifo *et al.* (1997), Salaman & Mazariegos (1998a), Snow & Snow (1980), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Wege & Long (1995).

216. Collared Inca

Coeligena torquata

French: Inca à collier **German:** Brustband-Andenkolibri **Spanish:** Inca Acollarado
Other common names: White-cravat Hummingbird

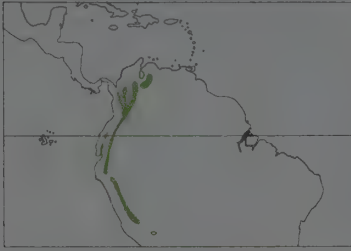
Taxonomy. *Ornismia torquata* Boissonneau, 1840. Bogotá, Colombia.

Relationships uncertain within the complex containing *C. wilsoni*, *C. prunellei*, present species and *C. inca*; further studies needed. Forms superspecies with *C. torquata*, with which traditionally considered conspecific; however, probably best considered separate species, on the basis of differences in plumage coloration, together with disjunct distributions. "*C. traviesi*" and "*C. lawrencei*" are most likely hybrids between present species and, respectively, *C. lutetiae* and *Lafresnaya lafresnayi*. Six subspecies recognized.

Subspecies and Distribution.

C. t. conradi (Bourcier, 1847) - Andes of NW Venezuela (Trujillo, Mérida) and E Andes of Colombia.
C. t. torquata (Boissonneau, 1840) - Andes of NW Venezuela (Táchira) through Colombia and E Ecuador to N Peru.
C. t. fulgidigula (Gould, 1854) - W Andean slopes of Ecuador.

C. t. margaretae Zimmer, 1948 - Andes of N Peru (Chachapoyas).
C. t. insectivora (Tschudi, 1844) - Andes of C Peru.
C. t. eisenmanni Weske, 1985 - S Peru (Cordillera Vilcabamba).



Descriptive notes. c. 14.5 cm; male c. 7.3 g, female c. 6.6 g. Male has long, straight, black bill; head black with dark purple crown spot; upperparts blackish-green, becoming green on lower back, postocular spot white; chin and throat black with green discs, broad white collar, underparts blackish-green, undertail-coverts washed green; tail forked, inner rectrices dark golden green, others white with contrasting dark golden green tips varying in size. Female has bill longer than male; head washed green lacking purple crown spot, upperparts shining golden green; chin grey with some green discs; large white collar, belly

dark grey with some golden green discs; undertail-coverts grey-green, fringed white; tail less forked. Immature similar to adult female, head feathers with buffy fringes. Race *conradii* very distinct from all other races in that male has no black on head, entire plumage shining grass green, white collar most extensive, tail more greenish, less bronzy, outer primaries edged rufous, female has throat rufous with some green discs; male of race *fulgidigula* similar to nominate but with crown bluer, less violet, upperparts slightly lighter blackish-green, throat patch large and shining turquoise green, collar narrower, belly green, female has upperparts glittering golden green, throat with green discs, collar narrow, belly dark grey with more green discs than in nominate; *margaretae* male has two spots on crown separated by a black line, front spot small and bluish, hind spot greenish, mantle more blackish, throat light and greener than in *fulgidigula* and nominate, female is similar to that of nominate and *fulgidigula*; *insectivora* male lacks the frontal patch, crown spot light green, mantle green with black, female similar to nominate; male of race *eisenmanni* has head black with green crown spot, upperparts and underparts shining green, uppertail-coverts shining coppery, central pair of rectrices bronzy-green, remaining rectrices white tipped bronzy-green, female green with some black on sides of head, throat rufous.

Habitat. Understorey to lower canopy of humid montane cloudforest, forest borders and occasionally in sub-*páramo*, mainly at 2200–3000 m, sometimes lower at 1500 m. Replaced ecologically at lower altitude by *C. coeligena*, though both species can occur sympatrically.

Food and Feeding. Nectar of flowering *Bomarea carderi*, *Cavendishia pubescens*, *C. guatapeensis*, *Fuchsia*, *Loasa*, *Macrocapaea*, *Palicourea demissa*, *P. vagrans* and *Vriesea*. Feeds by trap-lining in understorey to lower middle strata, sometimes in canopy, at forest edges or within dense vegetation. Where sympatric with *C. prunellei* it is subordinate to that species and is chased away from flowers. Catches arthropods by hawking or gleaning from foliage.

Breeding. Nov–Mar (Colombia). Cup-shaped nest hidden under ferns on rock cliffs 1.5–2 m above ground. Nest constructed of plant fibres and heavily decorated with yellowish-green moss and dead fern leaves on the outside. Clutch size 2; incubation by female. No further information.

Movements. No information available, but possibly undertakes seasonal short-distance movements and dispersal after reproduction.

Status and Conservation. Not globally threatened. CITES II. Very common throughout much of range. To date no threats have been recorded, but since its habitat, humid montane cloudforest, is under heavy threat of destruction, species could suffer in the near future. Does not seem to take to man-made habitats or otherwise disturbed areas. Large areas of its habitat are protected, such as Munchique National Park (Colombia) and Paschoa Forest Reserve and North Podocarpus National Park (Ecuador). Has been imported regularly into Europe over recent decades, but rate of importation has decreased following tightening of national and international regulations; wild-bird trade does not seem to have had a severe impact on populations.

Bibliography. Baez *et al.* (1997), Best *et al.* (1997), Bloch *et al.* (1991), Butler (1979), Davies *et al.* (1994), Fjeldså & Krabbe (1990), Hilty & Brown (1986), Kraemer & Schmitt (1991), Meyer de Schauensee & Phelps (1978), Parker *et al.* (1982), Remsen (1985), Ridgely & Gaulin (1980), Rusch (1961d), Rutgers & Norris (1972), Schuchmann (1980d), Snow & Snow (1980), Stotz *et al.* (1996), Weske (1985), Wiedenfeld (1985), Williams & Tobias (1994), Zimmer (1948, 1951a).

217. Gould's Inca

Coeligena inca

French: Inca de Gould **German:** Inkaandenkolibri **Spanish:** Inca de Gould

Taxonomy. *Bourcieria inca* Gould, 1852, Coroico, Bolivia.

Relationships uncertain within the complex containing *C. wilsoni*, *C. prunellei*, *C. torquata* and present species; further studies needed. Forms superspecies with *C. torquata*, with which traditionally considered conspecific; however, probably best considered separate species, on the basis of differences in plumage coloration, together with disjunct distributions. Race *omissa* doubtfully valid, as the characters distinguished are very weak and not constant. Two subspecies currently recognized.

Subspecies and Distribution.

C. i. omissa Zimmer, 1948 - Andes of SE Peru (Urubamba to Puno).

C. i. inca (Gould, 1852) - Andes of Bolivia (La Paz, Cochabamba).



Descriptive notes. c. 14.5 cm; 6.8–7.2 g. Male has long, straight, black bill; head black with green frontlet, postocular spot white; upperparts golden green, becoming more shiny green on lower back; uppertail-coverts golden green; throat black with some green discs; collar rufous instead of white as in *C. torquata*, belly golden green; undertail-coverts light golden green, fringed white; tail forked, central pair of rectrices bronzy-green, remainder white with bronzy-green tips. Female has longer bill than male; head black, lighter than in male with golden green discs, upperparts shining golden green; collar rufous with some

green discs on sides, lower underparts washed rufous with large golden green discs; tail less forked. Immature resembles adult female. Male *omissa* differs from nominate in bluish rather than green frontlet, back and lower underparts dark green, throat is more pronounced green; female not distinguishable from nominate.

Habitat. Understorey and lower canopy of wet montane forest, at 1600–3200 m. Forages inside forest and along trails.

Food and Feeding. Takes nectar of flowering epiphytic ericads, vines, climbers and bromeliads, mainly with long tubular pendent corollas. Insects and other arthropods are caught by hawking or gleaning. Feeds on nectar by trap-lining.

Breeding. No information available.

Movements. No information available.

Status and Conservation. Not globally threatened. CITES II. Locally common. Part of range is protected by nature reserves and national parks. No evidence available at present that species can adapt to man-made habitats.

Bibliography. Bond & Meyer de Schauensee (1943), Fjeldså & Krabbe (1989, 1990), Hinojosa *et al.* (1998), Olrog (1968), Remsen (1985), Remsen & Taylor (1989), Weske (1985), Zimmer (1948, 1951a).

218. White-tailed Starfrontlet

Coeligena phalerata

French: Inca à queue blanche **German:** Weißschwanz-Andenkolibri **Spanish:** Inca Coliblanco

Taxonomy. *Leucuria phalerata* Bangs, 1898, Macotama; error = San Miguel, Santa Marta Mts, Colombia.

Monotypic.

Distribution. Santa Marta Mts (NE Colombia).



Descriptive notes. c. 14 cm. Male has long, straight, black bill; head and crown glittering turquoise, small white postocular spot; upperparts metallic dark green; underparts emerald green with blue throat patch, white leg puffs, undertail-coverts white; tail forked, white, bronze tips disappearing with age. Female has longer bill than male, upperparts shining green, crown dusky blue-green, small white postocular spot; underparts uniform rufous cinnamon; tail less forked, bronzy with small, pale buff tips. Immature resembles adult female.

Habitat. Interior and borders of humid and wet montane forest at 1400–3700 m. Slight differences between sexes in habitat choice recorded; male prefers openings in forest interior while females outnumber males at forest borders.

Food and Feeding. Feeds on nectar of flowering *Fuchsia*, bromeliads, banana and probably of a similar range of flowers as other *Coeligena*. Arthropods are taken by gleaning or hawking. More territorial than other *Coeligena*; occasional trap-liner.

Breeding. Feb–Apr based on gonadal condition of specimens. No further information available.

Movements. No information available.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Santa Marta Mountains EBA. Generally common. This species is endemic to the Santa Marta Mts, the natural habitats of which, although largely protected, are under severe threat of deforestation. Species is not known to accept man-made habitats or even slightly disturbed areas. Urgent need for further investigation.

Bibliography. Fjeldså & Krabbe (1990), Hilty & Brown (1986), Meyer de Schauensee (1982), Norton (1975), Olrog (1968), Salaman & Mazariegos (1998a), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Todd & Carriger (1922).

219. Golden Starfrontlet

Coeligena eos

French: Inca doré **German:** Goldandenkolibri **Spanish:** Inca Alirrufo

Taxonomy. *Helianthea Eos* Gould, 1848, higher altitudes of the Sierra de Mérida, Venezuela. Probably forms a superspecies with *C. bonapartei*, *C. helianthea*, *C. lutetiae* and *C. violifer*; traditionally considered a race of *C. bonapartei*, but probably best considered a separate species on the basis of plumage characters. Monotypic.

Distribution. Andes of W Venezuela, in Trujillo, Barinas, Mérida and Táchira.



Descriptive notes. c. 14 cm; male c. 6.8 g, female c. 6.4 g. Male has long, straight, black bill, shorter than in other *Coeligena*; plumage characters are similar to *C. violifer*; head blackish-green with green frontlet, small white postocular spot, upperparts golden green becoming glittering golden on rump; throat emerald green with violet throat patch, belly yellowish-green to golden orange; dark wing with cinnamon secondaries fringed dark brown, outer primary edged rufous; undertail-coverts light cinnamon, tail forked, cinnamon tipped golden bronzy. Female has longer bill than male; greenish head, upperparts similar

to male; cinnamon buff chin with green discs; belly glittering, less golden orange; tail less forked. Immature resembles adult female.

Habitat. Cloudforest and dwarf forest, openings with scattered vegetation, sometimes near *páramo* at 1400–3200 m. Forages at periphery of vegetation, usually very low down, at 2–3 m.

Food and Feeding. Feeds on nectar of flowering *Bomarea*, *Cavendishia*, *Fuchsia*, *Macleania*, *Mutisia* and *Palicourea*. Gleans, and occasionally hawks for arthropods. Feeds by trap-lining from lower to middle strata in trees around edge of thickets.

Breeding. Jan–Mar. Nest cup-shaped, made of moss, lichens and rootlets, lined with soft plant material such as fibres of Bromeliad seeds, attached to vertical branches inside vegetation. No further information.

Movements. Possibly seasonal altitudinal dispersal after breeding and following flowering food plants.

Status and Conservation. Not globally threatened. CITES II. Range is protected by two national parks and there is at present no threat of deforestation. Species is not known to accept man-made habitats.

Bibliography. Fjeldså & Krabbe (1990), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Olrog (1968), Stattersfield *et al.* (1998).

220. Golden-bellied Starfrontlet

Coeligena bonapartei

French: Inca de Bonaparte **German:** Goldbauch-Andenkolibri **Spanish:** Inca Ventriderado
Other common names: Dusky Starfrontlet (*orina*)

Taxonomy. *Ornismia bonapartei* [sic] Boissonneau, 1840, Bogotá, Colombia. Probably forms superspecies with *C. eos*, *C. helianthea*, *C. lutetiae* and *C. violifer*; traditionally considered to include *C. eos* as race, but probably best considered separate species on the basis of plumage characters. Taxon *orina*, known from single specimen (probably an immature male), is often considered a separate species; however, it may be best considered a race of present species, or it may even represent some melanistic plumage. Three subspecies recognized.

Subspecies and Distribution.

C. b. consita Wetmore & Phelps, Jr., 1952 - Sierra de Perijá, along Colombia-Venezuela border.

C. b. bonapartei (Boissonneau, 1840) - E Andes of Colombia (Boyacá S to Bogotá).

C. b. orina Wetmore, 1953 - Páramo de Frontino in Antioquia (NC Colombia).



Descriptive notes. c. 14 cm; 6.4-6.9 g. Male has long, straight, black bill; head black with green iridescent frontlet slightly more bluish than in *C. eos*, postocular spot white; upperparts shining dark green, more golden orange on rump, uppertail-coverts dark golden bronze; throat glittering dark emerald green with iridescent violet patch, more bluish than in *C. eos*, belly golden, undertail-coverts golden bronze fringed rufous; tail forked, dark golden bronze. Female similar to male, bill longer; head green; chin and throat rufous with some green discs; underparts rufous with large green discs, golden on vent, undertail-coverts bronzy-green, largely

fringed rufous; tail less forked, golden bronze, sometimes buff on tip. Immature resembles adult female. Male of *consita* similar to nominate but has rufous band across secondaries contrasting with dusky rest of wing, tail slightly brighter golden bronze, female similar to nominate apart from rufous band on wing; male of doubtful race *orina* very dark, almost black with a weak green sheen, lacking bronzy and cinnamon, small bluish gular spot, female unknown.

Habitat. Cloudforest and dwarf forest, open terrain with scattered vegetation at 1400-3200 m.

Food and Feeding. Flowers visited for nectar include *Bomarea*, *Cavendishia*, *Fuchsia*, *Macleania*, *Mutisia* and *Pulicourea*. Hawks in the air for insects and gleans arthropods from plant surfaces. Feeds mainly by trap-lining low down on outer edges of medium to tall shrubs.

Breeding. Jan-Jul. No further information.

Movements. No information but altitudinal dispersal likely.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Cordillera de Mérida EBA and Colombian East Andes EBA. Generally common. Race *bonapartei* has a wide distribution, but *consita* and *orina* very restricted in range. Perijá Mts (*consita*) are situated on the Venezuela-Colombia border, where much illegal activity takes place, such as of new settlements. The region does not coincide with any protected areas, and numerous roads approaching Perijá Mts from Colombian territory imply further interest by people in colonizing the area and the exploitation of minerals; some parts of range are still pristine, however. All races seem to accept habitat disturbance by man to some extent.

Bibliography. Bleiweiss (1988b), Carrier (1954), Fjeldså & Krabbe (1990), Hilty (1985), Hilty & Brown (1986), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Olrog (1968), Salaman & Mazariegos (1998a), Stattersfield *et al.* (1998), Siles & Wolf (1974), Stotz *et al.* (1996), Wetmore (1953), Wetmore & Phelps (1952).

221. Blue-throated Starfrontlet

Coeligena helianthea

French: Inca porphyre **German:** Rosenbauch-Andenkolibri **Spanish:** Inca Ventrivioleta

Taxonomy. *Ornismia helianthea* Lesson, 1838, Bogotá, Colombia.

Probably forms superspecies with *C. eos*, *C. bonapartei*, *C. lutetiae* and *C. violifer*. Race *tamai* sometimes misspelt "*tamae*". Two subspecies recognized.

Subspecies and Distribution.

C. h. helianthea (Lesson, 1838) - N & E Andes of Colombia (Sierra de Perijá to Bogotá).

C. h. tamai Berlioz & Phelps, 1953 - Páramo de Tamá in Táchira (W Venezuela).

Descriptive notes. c. 13 cm; male 7.1-7.6 g, female 6.6-5 g. Male has long, straight, black bill; head black with dark green frontlet, postocular spot white, upperparts dark with slight emerald green gloss, lower back and rump dark blue with some violet; underparts dark grey with emerald



green sheen, dark iridescent violet throat patch, lower underparts shining rosy including undertail-coverts; tail forked, bronzy-black. Female similar to male, bill longer; head grey-green, upperparts golden green becoming blue-violet on rump but not as conspicuous as in male; throat rufous, breast rufous with green discs, belly rosy, undertail-coverts lighter, without rosy sheen; tail less forked, dark bronzy-black. Immature similar to adult female. Male of race *tamai* is duller, belly and undertail-coverts more bluish, less rosy; female similar to nominate.

Habitat. Cloudforest and dwarf forest, forest edge, shrubby slopes, also visits flowering gardens. Occasionally in more open terrain and in bushy sub-páramo at 1900-3300 m.

Food and Feeding. Food plants visited for nectar include *Befaria*, *Bomarea*, *Cavendishia cordifolia*, *Elleanthus*, *Fuchsia*, *Macleania*, *Macrocarpea*, *Symbolanthus* and *Tropaeolum*. Individuals have been seen taking nectar from long corollas of *Passiflora mixta* using holes pierced by White-sided Flowerpiercer (*Diglossa albilatera*) at the flower base. Insects are usually caught by gleaning from foliage, sometimes by hawking. Feeds by trap-lining in lower strata.

Breeding. May-Oct. No further information available.

Movements. Unknown, but seasonal altitudinal dispersal likely.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Colombian East Andes EBA. Locally common. This species is probably more able than its congeners to accept disturbed areas and man-made habitats; not so closely tied to cloudforest as other *Coeligena* species; nevertheless, its natural habitat is under threat of deforestation.

Bibliography. Fjeldså & Krabbe (1990), Hilty & Brown (1986), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Olrog (1968), Snow & Snow (1980), Stattersfield *et al.* (1998), Stotz *et al.* (1996).

222. Buff-winged Starfrontlet

Coeligena lutetiae

French: Inca à gemme bleue **German:** Fahlflügel-Andenkolibri **Spanish:** Inca Alihabano
Other common names: Compte de Pario/Conte de Paris' Starfrontlet

Taxonomy. *Trochilus Lutetiae* Delattre and Bourcier, 1846, Puracé Volcano, near Popayán, Colombia. Probably forms superspecies with *C. eos*, *C. bonapartei*, *C. helianthea* and *C. violifer*. "*C. traviesti*" is most likely a hybrid between present species and *C. torquata*. Monotypic.

Distribution. C Andes of Colombia through Ecuador to extreme N Peru.



Descriptive notes. c. 14 cm; male 6.9-7.2 g, female c. 6.6 g. Male has long, slightly upturned, black bill; upperparts velvety black with green glittering frontlet, postocular spot white; underparts dark green with violet throat patch; wings dark with obvious cinnamon buff secondaries; tail forked, bronzy-black. Female shining dark green above, with cinnamon buff patch apparent on wing, as in male; throat cinnamon buff, below golden green with pale feather fringes; tail less forked, more bronzy-green. Immature resembles adult female.

Habitat. From dense cloudforest to *Polylepis* woodland in sub-páramo at 2600-3600 m, com-

monest around 3000 m.

Food and Feeding. Flowers visited for nectar include mistletoes, *Bomarea*, *Cavendishia* and *Fuchsia*. Arthropods are caught by hawking and gleaning. Trap-liner, foraging at lower level at forest edges; often perches near flowers while feeding.

Breeding. Aug-Sept (C Andes, Colombia). Bulky cup-shaped nest of moss constructed 2-4 m above ground in forked branches. Clutch size 2; incubation 15-17 days, by female.

Movements. Sedentary, most likely some seasonal dispersal following flowering.

Status and Conservation. Not globally threatened. CITES II. Uncommon to locally common. *Polylepis* woodlands and sub-páramo zones are under severe threat of deforestation. Distribution patchy and fragmented; species not likely to accept man-made habitats. Occurs in North Podocarpus National Park (Ecuador). Biology and ecology of species very poorly known; research required. In the past, individuals were imported into Europe on a regular basis in the wild-bird trade, but this has now ceased as a result of national and international regulations.

Bibliography. Baez *et al.* (1997), Best *et al.* (1997), Bloch *et al.* (1991), Butler (1979), Fjeldså & Krabbe (1990), Hilty & Brown (1986), Krabbe *et al.* (1997), Kraemer & Schmitt (1991), Parker *et al.* (1985), Poulsen (1996), Rutgers & Norris (1972), Salaman & Mazariegos (1998b), Schuchmann (1980d), Stotz *et al.* (1996), Vélez & Velázquez (1998), Williams & Tobias (1994), Zimmer (1951a).

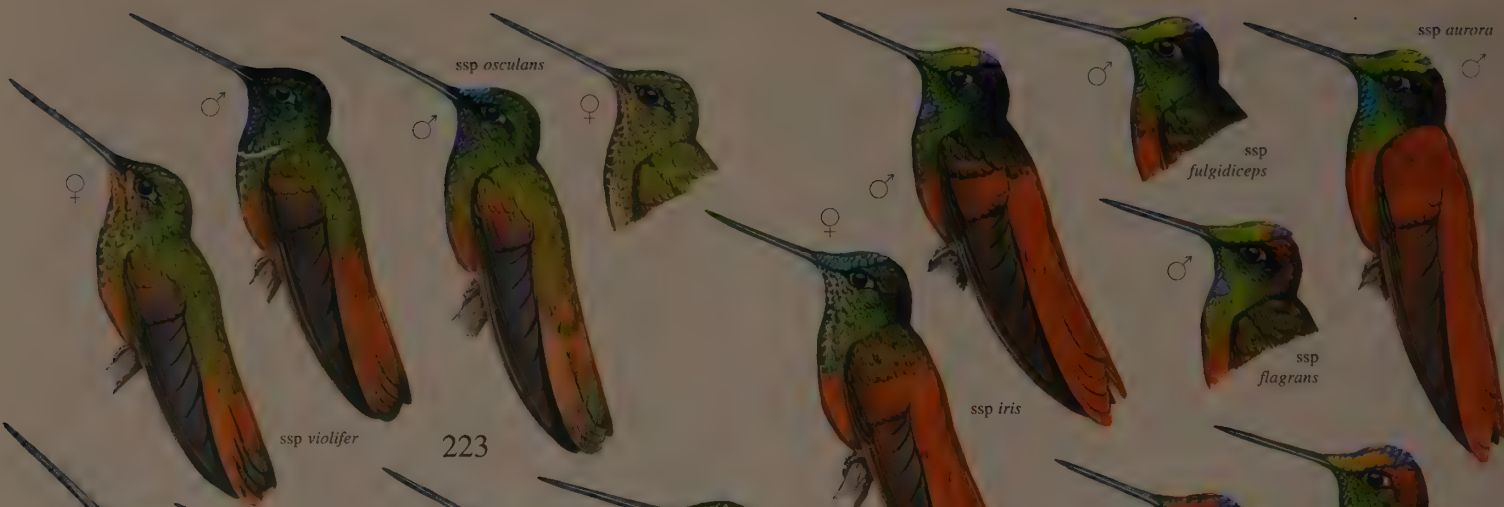


PLATE 65

inches 2

cm 5

223. Violet-throated Starfrontlet

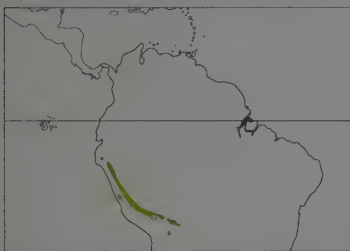
Coeligena violifer

French: Inca violifère **German:** Veilchenkehl-Andenkolibri **Spanish:** Inca Gorgimorado

Taxonomy. *Trochilus* (—?) *violifer* Gould, 1846, Sandillani Road, Yungas, Bolivia. Probably forms superspecies with *C. eos*, *C. bonapartei*, *C. helianthea* and *C. lutetiae*. Four subspecies recognized.

Subspecies and Distribution.

- C. v. dichroua* (Taczanowski, 1874) - S Ecuador (Loja) and E Andes of N & C Peru; relict population in W Peru (Lima).
- C. v. albicaudata* Schuchmann & Züchner, 1997 - Apurímac region (S Peru).
- C. v. osculans* (Gould, 1871) - E Andes of SE Peru (SE of Urubamba).
- C. v. violifer* (Gould, 1846) - E Andes of NW Bolivia.



Descriptive notes. 13-14.5 cm; male 6-11.5 g, female 5-6-8-6 g. Male has long, straight, black bill; head blackish-blue, postocular spot white, back shining bronzy-green; throat and breast green with iridescent violet gular spot, thin greyish band across upper breast, lower breast green contrasting with cinnamon belly and undertail-coverts; tail forked, uniform orange-buff with small bronzy tips. Female similar to male, bill longer; head green; throat buff with green discs, breast marked darkish green becoming rich cinnamon on belly; tail less forked. Immature resembles adult female. Male of race *dichroua* has forehead patch more bluish, indication of whitish band across breast, tail has broad bronzy terminal band, female similar but lacking frontlet and gular patch, significantly heavier than all other races; *albicaudata* has frontlet turquoise, throat patch more bluish-purple, conspicuous white undertail-coverts and whitish tail, distally faded green, central pair of rectrices entirely dark faded green, tail becoming whiter with age, female similar to nominate but with same tail coloration as male; male of *osculans* has frontlet intense greenish turquoise, crown dark shining green, gular spot variable, somewhat intermediate between nominate and *dichroua*, lower underparts and undertail-coverts pale cinnamon, tail like *dichroua* but with less extensive bronzy terminal band, female lacks frontlet and throat patch.

Habitat. Edges and clearings of cloudforest and elfin forest, sometimes in second growth, at 1300-3700 m, commonest at 2800-3300 m.

Food and Feeding. Nectar of flowering *Virola*, *Fuchsia* and *Bomarea*. Arthropods are caught by glean or hawking. Feeds by trap-lining low down along periphery of vegetation, occasionally inside forests along trails.

Breeding. Nov-Jan. No further information available.

Movements. Wide altitudinal range and only occasional occurrence below 2800 m suggest some seasonal dispersal over different elevations, possibly following flowering season. In certain months (Oct-Dec, Tamiapampa, N Peru) altitudinal separation between males and females has been observed.

Status and Conservation. Not globally threatened, CITES II. Habitat partially under threat of deforestation; species has not been recorded in man-made habitats, but since it inhabits open forest and clearings, it may accept these disturbed areas to some extent.

Bibliography. Bertioz (1936a), Bond & Meyer de Schauensee (1943), Davies *et al.* (1994), Elliot (1874), Fjeldså & Krabbe (1989, 1990), Hinojosa *et al.* (1998), Koepcke (1970), Meyer de Schauensee (1982), Parker *et al.* (1982), Remsen (1985), Remsen & Traylor (1989), Remsen, Traylor & Parkes (1986), Schuchmann (1980d), Schuchmann & Züchner (1997), Stotz *et al.* (1996), Taczanowski (1884), Zimmer (1930, 1951a).

224. Rainbow Starfrontlet

Coeligena iris

French: Inca iris **German:** Grünroter Andenkolibri **Spanish:** Inca Arcoiris
Other common names: King Louis (XVI) Starfrontlet

Taxonomy. *Helianthea iris* Gould, 1854, eastern slope of the Andes.

A problem exists regarding nomenclature of race *aurora*: description of name *warzewiczii* [sic] obviously describes the same race, but described in same year and cannot be dated exactly to the month; in absence of clarification, *aurora* has become the accepted name. Proposed race *hypocrita* (Chachapoyas), based on immature plumage, is synonym of *fulgidiceps*. Six subspecies recognized.

Subspecies and Distribution.

- C. i. hesperus* (Gould, 1865) - SW Ecuador (Cuenca).
- C. i. iris* (Gould, 1854) - S Ecuador (Loja) to N Peru (Piura).
- C. i. aurora* (Gould, 1854) - N Peru (Cuzco, Cerros de Amachonga).
- C. i. fulgidiceps* (Simon, 1921) - N Peru E of Marañón (Chachapoyas, Tamiapampa, Leimebamba, Levanto).
- C. i. flagrans* Zimmer, 1951 - NW Peru (Cajamarca).
- C. i. eva* (Salvin, 1897) - N Peru W of R Marañón on E slope of W Andes (Cajamarca, La Libertad).



Descriptive notes. 12-15 cm; male 8-11 g, female c. 8-1 g. Male has long, straight, black bill; head black with fiery glittering yellowish-green forecrown passing through golden yellow to blue, postocular spot white, upperparts blackish with slight green sheen, lower upperparts chestnut; throat glittering emerald green with small violet gular spot, lower underparts and undertail-coverts chestnut; tail forked, uniform chestnut. Female similar to male, bill longer and overall coloration less metallic; tail less forked. Immature similar to adult female. Male of race *hesperus* has crown dark golden red with blue central stripe, back golden green, underparts green with small violet gular patch, tail chestnut with bronzy tips, female similar but duller on hindcrown and underparts; male *aurora* has turquoise crown with golden feather tips, hindneck black, rest of

upperparts uniform light chestnut, chin and throat turquoise, rest of underparts uniform light chestnut, female similar but with less "fiery" coloration; *flagrans* similar to nominate, hindneck and back coppery, hindcrown tinged red; *fulgidiceps* also like nominate, with neck and upper mantle blackish, generally darker chestnut; male *eva* has forecrown yellowish-green, central crown dark violet, hindneck and back coppery, chin, throat and breast emerald green, lacking violet gular patch, rest of underparts chestnut, female similar but with coppery green head, underparts lighter than male.

Habitat. Edges of humid and drier cloudforest, gardens and riparian scrub, at 1700-3300 m. Forages low down, at 2-4 m above ground.

Food and Feeding. Feeds on nectar at a great variety of flowers, including *Embothrium*, *Fuchsia*, *Lochroma*, *Mutisia*, *Salvia*, *Siphocampylus giganteus* and *Tilandsia* by trap-lining; sometimes recorded at introduced *Eucalyptus* trees. Insects are caught in the air by hawking.

Breeding. Nov-Jan. Cup-shaped nest is constructed of moss, lichens and some small twigs, lined with soft plant material like fibres from bromeliad seeds, placed in fork of small branch. No further information.

Movements. Presumably sedentary.

Status and Conservation. Not globally threatened, CITES II. Restricted-range species: present in Southern Central Andes EBA. Locally common but may be vulnerable due to very restricted range. Natural habitat under threat of deforestation and heavily fragmented. This species seems to accept man-made habitats to some extent, particularly flowering gardens and park-like landscapes. In Ecuador, occurs in Las Cajas National Recreation Area and North Podocarpus National Park.

Bibliography. Best & Clarke (1991), Best, Clarke *et al.* (1993), Best, Heijnen & Williams (1997), Bloch *et al.* (1991), Butler (1979), Collar & Andrew (1988), Davies *et al.* (1994, 1997), Fjeldså & Krabbe (1990), Gretton (1986), King (1988, 1989, 1991), Parker *et al.* (1982), Poulsen (1996), Remsen & Traylor (1989), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Taczanowski (1884), Williams & Tobias (1994), Zimmer (1951a).

Genus *ENSIFERA* Lesson, 1843

225. Sword-billed Hummingbird

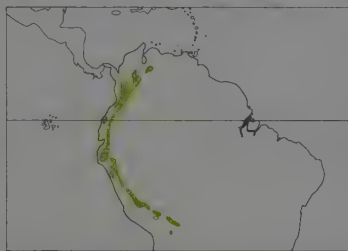
Ensifera ensifera

French: Colibri porte-épée **German:** Schwertschnabelkolibri **Spanish:** Colibri Picoespada

Taxonomy. *Ornismya ensifera* Boissonneau, 1840, Bogotá, Colombia.

Closely related to *Coeligena* and may even belong in that genus. Proposed race *caerulescens*, known from a single specimen of unknown origin, is apparently not valid, as morphological differences are most likely aberrant and may even relate to a damaged skin. Monotypic.

Distribution. Andes from W Venezuela through Colombia, Ecuador and Peru to NE Bolivia.



Descriptive notes. 17-22.8 cm (including bill of 9-11 cm); 12-15 g. Longest bill of any hummingbird; straight to slightly upturned, black. Male is dark green, head coppery, postocular spot white; throat blackish, underparts glittering emerald green, belly dark grey; tail forked, blackish. Female similar to male, has underparts lighter with throat and belly washed grey with green discs; tail less forked. Immature resembles female.

Habitat. Humid to semi-humid upper montane forest and forest edges, sometimes at patches of shrubs in páramo, at 1700-3500 m, commonest at 2500-3000 m.

Food and Feeding. Flowers visited for nectar have long pendulous corollas, and include *Aethanthus*, *Fuchsia*, *Salpichroa*, *Solanum*, *Datura sanguinea*, *D. tatula*, *Passiflora mixta*, *Tacsonia pinnatistipula*, *T. mollissima* and *T. floribunda*. Hawks for insects in "swift-like" manner with wide open bill. Traps nectar for flowers in mid to upper strata; sometimes perches below flowers while feeding.

Breeding. No reliable information. One unconfirmed observation of a female defending a possible nesting site high up in a tree in Apr (Ecuador); another doubtful description records several moss nests 15 m above ground in a tree.

Movements. Sedentary. In Colombia, seasonally above 3000 m (Jul-Sept, C Cordillera, Colombia).

Status and Conservation. Not globally threatened, CITES II. Common locally. In Oyacachi (Bolivia) this hummingbird has been selected as a target species for ecotourism to attract birdwatchers, and these measures should help to protect its natural habitat from deforestation. In some places, it is known to take to man-made habitats like flowering gardens when suitable flowers are present, for example near Los Frailes Hotel in Venezuela, known to be an excellent spot to observe the bird. Around beginning of present century it was a common bird in suburbs of Quito. Occurs in several protected areas such as Munchique National Park (Colombia), and Pascocha Forest Reserve, Las Cajas National Recreation Area and North Podocarpus National Park (Ecuador).

Bibliography. Baer *et al.* (1997), Best *et al.* (1997), Bloch *et al.* (1991), Butler (1979), Cordier (1983), Fjeldså & Krabbe (1990), Graves (1991), Hilty & Brown (1986), Kraemer & Schmitt (1991), Linhart (1973), Lowe (1939), Meyer de Schauensee & Phelps (1978), Moore (1947a), Parker *et al.* (1982), Remsen (1985), Remsen & Traylor (1989), Richmond (1902), Ridgely & Gaulin (1980), Ruschi (1961b, 1973d), Rutgers & Norris (1972), Snow & Snow (1980), Stotz *et al.* (1996), Taczanowski (1884), Todd (1942), Walters (1986), Williams & Tobias (1994), Wittmann (1982), Zimmer (1930, 1951a).

Genus *PTEROPHANES* Gould, 1849

226. Great Sapphirewing

Pterophanes cyanopterus

French: Colibri à ailes saphir **German:** Blauflügelkolibri **Spanish:** Colibrí Aliazul
Other common names: Sapphirewing, Paramo/Temminck's Sapphirewing

Taxonomy. *Trochilus cyanopterus* Fraser, 1840, Bogotá, Colombia.

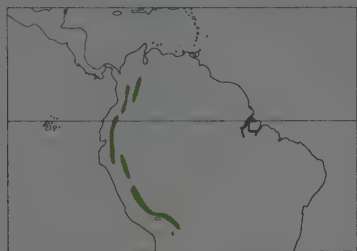
Genus closely related to *Coeligena*, and should perhaps be merged therein. Three subspecies recognized.

Subspecies and Distribution.

P. c. cyanopterus (Fraser, 1840) - E Andes of NC Colombia (Santander, Cundinamarca).

P. c. caeruleus Zimmer, 1951 - Colombia, in C Andes (S from Tolima) and extreme SW Andes (Nariño).

P. c. peruvianus Boucard, 1895 - Ecuador, Peru and N Bolivia.



Descriptive notes. Male 19-20 cm, female 16-17 cm; male 10-2-11-2 g, female 9-1-11 g. Bill straight, medium-sized, black. Male dark shining bluish-green above; rather long greenish-black tail deeply forked; wings very long, upperwing- and underwing-coverts, and proximal part of inner webs of primaries shining blue; underparts somewhat glittering bluish-green, including undertail-coverts. Female shining metallic green above, forehead dusky grey; tail shorter than in male and less forked, the lateral pair of rectrices with a pale median line on outer web; wing-coverts are blue as in male but primaries with less blue; underparts

cinnamon-rufous with green discs especially on flanks, undertail-coverts green. Immature bird resembles female, but with fewer green lateral spots. Race *caeruleus* differs from nominate by distinctly more and darker blue in general coloration, especially on wings, with blue colour reaching almost to tip of outermost primary, female also bluer, has a darker cap and a less prominent pale stripe on lateral rectrices than nominate; *peruvianus* has entire upperparts including tail lighter green, but birds from Ecuador are slightly bluish in overall coloration, almost approaching *caeruleus*, wings have extent of blue similar to *caeruleus*, below also lighter green, less blue, towards belly growing increasingly buffy (most evident in birds from Bolivia), female has underparts less cinnamon than nominate race, whitish median line on rectrices more marked.

Habitat. Inhabits humid and not too dense cloudforest and stunted forest borders, elfin woodland, and shrubby slopes with scattered trees in temperate zone near tree-line, but also more open grassy slopes in wet to sometimes rather dry zones well into páramo, at 2600-3700 m, commonest at c. 3000 m.

Food and Feeding. Takes nectar from flowers at low to moderate heights on the outside of thickets and bushes, either hovering or perching to feed, sometimes clinging momentarily to flowers. Usually alone, but may join mixed flocks of highland tanagers, flowerpiercers and warblers. Main food plants are *Barnadesia*, *Bomarea*, *Mutisia*, *Passiflora* and *Puya*; sometimes also feeds from larger herbs (*Centropogon*, *Loasa*, *Siphocampylus*). Territorial, but may occasionally also trap-line flowers. Insects are caught by hawking.

Breeding. Breeding has been recorded for Feb (Colombia) and May (Ecuador). Cup-shaped nest is suspended from roots or ferns, usually situated below vegetation cover, 2-4 m above ground. Clutch size 2; incubation 16-18 days, by female; fledging period 26-29 days.

Movements. Mainly sedentary; altitudinal movements to open páramo after reproduction.

Status and Conservation. Not globally threatened. CITES II. Locally fairly common. Less abundant in dry Andean valleys in Ecuador. Present in Las Cajas National Recreation Area, Ecuador.

Bibliography. Baez *et al.* (1997), Best *et al.* (1997), Bloch *et al.* (1991), Bond & Meyer de Schauensee (1943), Brown & Bowers (1985), Butler (1979), Davies *et al.* (1994), Fjeldså (1991), Fjeldså & Krabbe (1990), Hilty & Brown (1986), Hinojosa *et al.* (1998), King (1991), Koepcke (1970), Parker *et al.* (1982), Remsen (1985), Remsen & Traylor (1989), Snow (1983), Stotz *et al.* (1996), Zimmer (1930, 1951b).

Genus *PATAGONA* G. R. Gray, 1840

227. Giant Hummingbird

Patagona gigas

French: Colibri géant

German: Riesenkolibri

Spanish: Colibrí Gigante

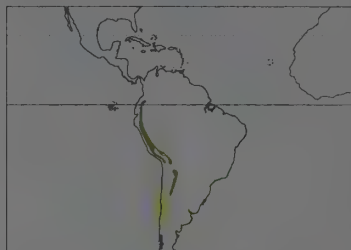
Taxonomy. *Trochilus gigas* Vieillot, 1824, Brazil; error = Valparaíso, Chile.

Genus is apparently closely related to *Coeligena*, and the two should perhaps be united. Two subspecies recognized.

Subspecies and Distribution.

P. g. peruviana Boucard, 1893 - Andes of SW Colombia (Nariño) through Ecuador, Peru and Bolivia to extreme N Chile (Tarapacá) and NW Argentina (S to N Catamarca and Tucumán).

P. g. gigas (Vieillot, 1824) - C & S Chile (Atacama to Concepción and Valdivia, occasionally S to Aisén) and CW Argentina (S to Mendoza); S populations winter N to NW Argentina (Catamarca, Tucumán).



Descriptive notes. 20-22 cm; 18.5-20.2 g, some birds may be over 23 g. Unmistakable, the largest hummingbird; hovers with very slow wingbeats, flight almost swift-like, occasionally interspersed with gliding. Bill black, straight and stout. Male upperparts dull olive-brown; rump conspicuously white with white edges to bronze-green uppertail-coverts; the forked, wedge-shaped tail is bronzy-olive with pale bases to rectrices, outermost feathers with central portion pale greyish; underparts and side of neck dull cinnamon, undertail-coverts contrasting white. Female has upperparts like male but generally tends to have underparts spotted dusky

grey to greater or lesser extent; some females very similar to male. Immature rufescent below with throat sometimes speckled grey; upperparts appear finely scaled, flight feathers are edged with white. Race *peruviana* differs from nominate in longer bill and wings, underparts are more cinnamon-rufous, rump less clearly white; female appears to be more constantly duller below than male.

Habitat. Favours arid, open habitats with low vegetation and few trees, usually not over 10 m in height. Typically to be found on shrubby steppe-like hillsides, often with thistles and many columnar cacti; in Ecuador and N Peru mainly agave-dominated areas and brushy canyons, often near small streams; generally prefers *Puya* or *Eucalyptus* stands and *Polylepis* and *Buddleia* woods, but also hedges and gardens near villages. Altitudinal distribution in Ecuador and N Peru chiefly 2000-3000 m, rarely up to 3300 m, the altitudinal limit of *Agave*; in Peru, Bolivia, Argentina and N Chile mainly at elevations of 2500-4000 m, but occasionally up to 4800 m in Peru, especially outside the dry season; in S Chile at much lower altitudes, from sea-level up to 2000 m.

Food and Feeding. In Ecuador and N Peru feeds mainly from *Agave* and *Puya* flowers; *Agave* was introduced to the area only in the 16th century, so a comparatively recent northward range expansion of this hummingbird is suspected to have taken place. Further south, where *Agave* is absent, the main nectar sources are *Puya*, *Opuntia cylindrica* and other tall cacti, also *Buddleia*, *Passiflora*, *Sittacanthus*, *Eucalyptus*, *Mutisia*, *Nicotiana* and *Lobelia*. Characteristically, the species is attracted to flowers that provide local aggregations of a few plants with abundant nectar supplies over short periods of time. Several individuals may gather at such locations of high flower density. While feeding, often perches or clings to a stem, hovering less frequently. Insects are typically obtained by hawking rather than hovering, though also employs sustained hovering to catch swarming insects. Notably aggressive and generally territorial.

Breeding. Mainly Dec-Mar (Ecuador), Sept-Mar (Peru) or Oct-Jan (Chile). Chilean populations sometimes have two clutches, the first about mid-Oct, the second in Dec-Jan. The tiny nest is built of moss and lichens held together with spider web, lined with sheep or plant wool and occasionally small feathers. Typically attached to a branch of a large bush or tree (especially poplar or eucalyptus), or on top of a cactus stem, mostly 2-4 m above ground. Clutch size 2, occasionally only 1; incubation 12-13 days, by female.

Movements. Populations of nominate race breeding in Chile and CW Argentina in spring and summer migrate across the Andes to adjacent Tucumán and Catamarca (NW Argentina) in autumn and winter. For the northern race *peruviana* there are so far only comparatively few breeding records from Ecuador, so it is still unclear whether the species breeds there regularly; after mid-Sept there is an increase in the population which is probably due to a migrant influx that might be correlated with *Agave* flowering. Apparently occurs only during Dec-Jan in SW Colombia (Nariño).

Status and Conservation. Not globally threatened. CITES II. Throughout its extensive range species is generally not uncommon. Does not seem to be restricted to threatened habitat types, and is often to be found in man-made environments. Occurs in several protected areas, e.g. Cotopaxi National Park (Ecuador) and Cerro La Campana National Park (Chile).

Bibliography. Babarskas *et al.* (1996), Barros (1952), Belmonte *et al.* (1994), Berlioz (1974), Bloch *et al.* (1991), Bond & Meyer de Schauensee (1943), Boucard (1893), Brown & Bowers (1985), Canevari *et al.* (1991), Chapman (1926), Contreras (1978), Cordier (1982), Fiameni (1986), Fjeldså (1991), Fjeldså & Barbosa (1983), Fjeldså & Krabbe (1990), Hellmayr (1932), Hilty & Brown (1986), Hüning (1999), Johnson (1967, 1972), King (1989), King & Holloway (1990), Krüger *et al.* (1982), Lasiewski *et al.* (1967), Marín *et al.* (1992), Miller (1985), Ortiz (1972, 1974), Pábler (1922), de la Peña (1994), Pereyra (1950), Prinzing *et al.* (1986), Remsen, Traylor & Parkes (1986), Rocha & Peharanda (1995), Ruschi (1949b, 1961a, 1964b), Rutgers & Norris (1972), Sahley (1996), Salaman & Mazariegos (1998b), Sanft (1970), Schuchmann & Jakob (1981b), Schuchmann & Prinzing (1987), Schuchmann *et al.* (1983), Spegazzini (1920), Stotz *et al.* (1996), Thompson D'Arcy (1901), Warncke (1993), Woods *et al.* (1998), Zimmer (1930, 1952), Zotta (1937).



Genus *SEPHANOIDES* G. R. Gray, 1840

228. Green-backed Firecrown

Sephanoides sephaniodes

French: Colibri du Chili

German: Chilekolibri

Spanish: Colibrí Austral

Taxonomy. *Orthorhynchus* [sic] *sephaniodes* Lesson, 1827, Bahía de Concepción Talcahuano, Chile. Genus seems to be closely related to a high-Andean lineage that includes *Lesbia*, *Metallura*, *Oreonympha* and *Oreotrochilus*. Sister-species relationship with *S. fernandensis* supported by recent DNA studies. Present generic name based on misspelling of species name; some recent authors have erroneously transferred spelling of generic name to species name, thus referring to "*Sephanoides sephaniodes*". In past, alternatively listed as *S. galeritus*, although the historical justification for this is doubtful since that name cannot be identified as present species. Monotypic.

Distribution. Chile (S of Atacama) and adjacent W Argentina (Neuquén to Santa Cruz) S to Tierra del Fuego; Juan Fernández Is. S populations winter N into EC Argentina.

Descriptive notes. 10-10.5 cm; male 5-5 g, female 5 g. Male has straight black bill; forehead and crown with distinctive iridescent fiery red-yellow; upperparts bronzy-green; underparts pale buff with brown-black and green spots fusing on sides; wings and tail slaty green. Female similar but lacks iridescent crown. Juvenile has rusty feather edges on head and is more cinnamon below.

Habitat. Forest edges, glades, thickets and gardens. Can be found in large numbers among flowering trees, including introduced species like *Eucalyptus*. From sea-level locally to above 2000 m.

Food and Feeding. Takes nectar from a variety of sources; most favoured are *Abutilon*, *Embothrium* and *Fuchsia*. On Juan Fernández found to use both introduced and native species, including *Dendroseris* and *Raphithamnus*.

Breeding. (Sept) Oct-Nov. On Is Juan Fernández few nests have been found but data suggest breeding Sept-Dec. Nests very small, cup-shaped, sometimes overhanging water; clutch size 2. No further information.

Movements. Migratory in southern region of the mainland, wintering in lowlands of Argentina. Juan Fernández population thought to be sedentary.

Status and Conservation. Not globally threatened. CITES II. Locally common; does well in disturbed habitats, occurring regularly in city parks, e.g. Santiago. No immediate threat, although man-induced environmental pressures affecting hummingbirds in general such as habitat destruction, pollution and conifer plantations are thought to have a negative effect. Occurs in several protected areas such as Cerro La Campana, Nahuelbuta and Puyehué National Parks (Chile). Range extended to Alejandro Selkirk I (Juan Fernández Is) in 1981, presumably by birds from neighbouring Robinson Crusoe I. Total numbers in Juan Fernández Is estimated at c. 5000 birds (4000-8000).

Bibliography. Araya & Chester (1993), Bennet (1931), Brooke (1987), Busse (1971), Canevari *et al.* (1991), Clark (1986), Colwell (1989), Delhey (1992), Estades (1995), Fjeldså & Krabbe (1990), Fraga *et al.* (1997), Humphrey *et al.* (1970), Johnson (1967), King (1839), López-Calleja & Bozinovic (1995), Martínez del Río (1992), Narosky & di Giacomo (1993), Narosky & Yzuriet (1993), Olrog (1984), Ortiz (1986), de la Peña (1994), Pereyra (1950), Prinzing *et al.* (1992), Ralph (1985), Reed (1874, 1883), Roy *et al.* (1998), Rozzi *et al.* (1996), Sclater (1871), Smith-Ramírez (1993), Stotz *et al.* (1996), Vuilleumier (1985), Wetmore (1926), Woods (1988), Zotta (1934).

229. Juan Fernandez Firecrown

Sephanoides fernandensis

French: Colibri robinson

German: Juan-Fernandez-Kolibri

Spanish: Colibrí de Juan Fernández

Other common names: Fernandez Firecrown

Taxonomy. *Trochilus fernandensis* King, 1831, Juan Fernández Islands.

Genus seems to be closely related to a high-Andean lineage that includes *Lesbia*, *Metallura*, *Oreonympha* and *Oreotrochilus*. Sister-species relationship with *S. sephaniodes* supported by recent DNA studies; in past, phylogenetic affinities with other hummingbird species have been much disputed. In mid-19th century, pronounced sexual dimorphism caused the sexes to be classified as two different species within the same genus, until observations of mating and of the two morphotypes sharing the same nest revealed their true identities. Race *leyboldi* of Alejandro Selkirk I (also Juan Fernández Is) is now extinct; originally considered a separate species. One extant subspecies recognized.

Subspecies and Distribution.

S. f. fernandensis (King, 1831) - Robinson Crusoe I in Juan Fernández Is (off WC Chile).

Descriptive notes. Male 11.5-12 cm, 10-9 g; female c. 10.5 cm, 6-8 g. Male has straight black bill; forehead and crown iridescent fiery reddish-yellow; upperparts, underparts and tail cinnamon-orange; wings dark coppery grey. Female has iridescent bluish-purple crown; upperparts bluish-green; underparts snow-white dappled with black and green discs; wings slaty green; central retrices and inner webs of outer retrices blue-green, inner webs of the latter white. Immature male crown increases in size and iridescence with age until adult; immature female has underparts rather more buff than adult.

Habitat. Forest, thickets and gardens, prefers shady and sheltered areas. Apparently well adapted to the native (and largely endemic) vegetation of Juan Fernández Is. Males found in relatively large numbers in the main street of San Juan Bautista during the summer when the *Dendroseris* trees are flowering.

Food and Feeding. Takes nectar from a variety of sources, preferring the endemic *Dendroseris littoralis* and *Raphithamnus venustus*; this latter may have co-adapted with the present species.



Introduced plants such as *Abutilon* and *Eucalyptus* also present potential food sources for this species. Prefers shaded flowers well above ground. Both sexes defend foraging territories, although the larger male tends to guard, quite fiercely, the most highly productive plants. "Crown-flashing", rasping calls and chasing play an important role in territorial disputes.

Breeding. Only a few nest records and virtually no data on breeding are available. Nests are small, placed well above ground in surrounding shelter; at least one was constructed from finely woven fern fibres.

Movements. Sedentary, although individuals

have been recorded moving all over Robinson Crusoe I, presumably in search of foraging territories. **Status and Conservation.** CRITICALLY ENDANGERED. CITES II. Restricted-range species; present in Juan Fernández Islands EBA. Situation critical; population estimated at only 250-400 individuals restricted to Robinson Crusoe I. Species once inhabited both major islands of group, with an estimated population of several thousands in 19th century; last recorded on Alejandro Selkirk I in 1908; other reports from the 19th century indicate that present species was very abundant, in contrast to the uncommon *S. sephaniodes*. Several anthropogenic factors appear to be have contributed to its decline: widespread destruction of the natural flora over the past 200 years, especially wood-harvesting at lower elevations, has created a more disturbed and open habitat; most of the now depauperate natural flora co-evolved with its pollinator, and their mutual decline may act synergistically; introduced rabbits and goats reduce the natural vegetation cover, which in turn promotes erosion, and the effect of annual flooding increases this erosion, favouring the spread of the introduced bramble (*Rubus*) in small valleys (*quebradas*), where the plant has been increasing in density and extending its altitudinal range; bramble produces flowers that appear to be too small to provide sufficient energy for a hovering male, while in addition this plant infests and shades out regenerating forest; and introduced predators such as rats and cats may cause some losses. The archipelago constitutes an International Biosphere Reserve, which affords good protection under the auspices of CONAF, Chile. Apart from direct conservation action, a comprehensive ecological and genetic study should be carried out aimed at preserving this species and its natural habitat: these studies should include behaviour and ecological requirements, and further DNA studies to assess inbreeding depression and genetic variation within the remaining population.

Bibliography. Allen (1984), Araya & Chester (1993), Bourne *et al.* (1992), Brooke (1987), Busse (1971), Chapin (1936), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Colwell (1989), Johnson (1967), King (1839), Lack (1971), Meza (1989), Moseley (1879), Muñoz (1969), Pizarro (1969), Reed (1874, 1883), Roy *et al.* (1998), Sclater (1871), Skottsborg (1920-1956), Stattersfield *et al.* (1998), Stiles (1987), Stotz *et al.* (1996), Stuessy *et al.* (1984), Wege & Long (1995).

Genus *HELIANGELUS* Gould, 1848

230. Orange-throated Sunangel

Heliangelus mavors

French: Héliange mars

German: Orangekehl-Sonnennympe

Spanish: Colibrí de Marte

Taxonomy. *Heliangelus mavors* Gould, 1848, Cordilleras of Venezuela and Colombia.

Monotypic.

Distribution. NW Venezuela (S Lara to Táchira) and E Andes of Colombia (Norte de Santander to Boyacá).



Descriptive notes. 10-11 cm; 3.9-4.4 g. Bill blackish and straight. Male shining green above with a rather narrow glittering orange frontlet; throat and upper breast are glittering coppery orange, bordered below by a broad cinnamon-buff pectoral band; rest of underparts are buff, thickly spotted with golden green discs, especially on the lower breast and flanks; the tail is square with the central feathers golden green and the outer feathers dark bronze with pale tips. Female similar but has gorget rufous brown speckled buff. Immature resembles adult female, but young male soon develops a dusky brown throat.

Habitat. Edges of humid montane cloudforest and dwarf forest, open pastures and páramo slopes with bushes and scattered trees in upper subtropical and temperate zones. Also inhabits rather dry habitats with scanty second growth from 2000 to 3200 m.

Food and Feeding. The species is territorial at flower clusters, usually at low levels inside the forest or at forest edges. *Salvia* has been recorded as food plant. While foraging usually stays near cover; often clings to flowers while feeding. Insects are caught by hawking.

Breeding. Dec-Mar. Clutch size 2, incubation by female. First breeding in second year. No further information available.

Movements. Mainly sedentary; altitudinal dispersal after breeding.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Cordillera de Mérida EBA and Colombian East Andes EBA. Locally common in the temperate zone of the Venezuelan Cordillera, especially with patches of páramo vegetation; generally uncommon to rare in Andes of NE Colombia, though frequently seen around Boyacá.

On following pages: 231. Longuemare's Sunangel (*Heliangelus clarisse*); 232. Amethyst-throated Sunangel (*Heliangelus amethysticollis*); 233. Gorgeted Sunangel (*Heliangelus strophianus*); 234. Tourmaline Sunangel (*Heliangelus exortis*); 235. Little Sunangel (*Heliangelus micraster*); 236. Purple-throated Sunangel (*Heliangelus viola*); 237. Royal Sunangel (*Heliangelus regalis*).

Bibliography. Bleiweiss (1994), Fjeldså & Krabbe (1990), Hilty & Brown (1986), Meyer de Schauensee (1949, 1982), Meyer de Schauensee & Phelps (1978), Olrog (1968), Stattersfield *et al.* (1998), Stotz *et al.* (1996).

231. Longuemare's Sunangel

Heliangelus clarisse

French: Héliange de Clarisse

Spanish: Colibrí de Clarissa

German: Longuemare-Sonnennympe

Other common names: Merida Sunangel (*spencei*)

Taxonomy. *Ornismya clarisse* Longuemare, 1841, Bogotá, Colombia.

Forms a superspecies with *H. amethysticollis*, with which formerly considered conspecific; however, subtle morphological differences and markedly disjunct range support their treatment as separate species; *H. strophianus* may also belong in this superspecies. Race *spencei* sometimes considered a distinct species, most typically when remaining races of present species are lumped into *H. amethysticollis*. Proposed race *verdiscutatus* (Páramo de Tamá) included within nominate, though possibly closer in plumage to *violiceps*. One case of hybridization has been recorded between present species and *Heliodoxa leadbeateri*. Form "dubius", known only from two trade skins, may be a melanistic form of present species. Three subspecies recognized.

Subspecies and Distribution.

H. c. violiceps Phelps & Phelps, Jr., 1953 - Sierra de Perijá, along Colombia-Venezuela border.

H. c. spencei (Bourcier, 1847) - Andes of Mérida (NW Venezuela).

H. c. clarisse (Longuemare, 1841) - E Andes of Colombia (Norte de Santander to Cundinamarca) and adjacent W Venezuela.



Descriptive notes. 10 cm; 5.0-6.0 g. Bill blackish and straight. Male shining dark bronzy-green above with dusky crown and a narrow glittering blue-green frontlet; throat and upper breast glittering rosy, forming the gorget typical for this genus, bordered below by a white pectoral band; remainder of the underparts are dusky buff spotted with green discs, especially laterally; the shallowly forked tail is dark bronzy-green centrally, with the outer rectrices blackish and occasionally with pale tips. Sexes are basically similar but female lacks the shining gorget; instead throat feathers are dull brown with rufous subter-

minal bar or a bronze-green fringe to the feather tips; belly usually less spotted with green. Immature resembles female. Race *violiceps* differs in having purplish crown and a strongly blue frontlet; in *spencei* the frontlet is more silvery green and the gorget more violet than rosy.

Habitat. Mainly inhabits borders of humid cloudforest and dwarf forest, but can occasionally be found in more open vegetation up to open páramo. Recorded at altitudes of 2000-3600 m.

Food and Feeding. Territorial. Usually forages at flowers at low to medium height.

Breeding. No information concerning breeding season. The nest consists of moss and fine plant material and is typically situated below some structure providing shelter. Clutch size 2; incubation by female. No further information.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Generally common; no potential threats identified to date. Race *spencei* sometimes considered full species and classified as restricted range species: present in Cordillera de Mérida EBA. This form occurs in Sierra Nevada National Park and at Santo Domingo Valley.

Bibliography. Bleiweiss (1994), Fjeldså & Krabbe (1990), Graves & Zusi (1990a), Hilty & Brown (1986), Meyer de Schauensee (1949, 1982), Meyer de Schauensee & Phelps (1978), Olrog (1968), Phelps & Phelps (1953), Salaman & Mazariegos (1998a), Snow & Snow (1980), Stattersfield *et al.* (1998), Stotz *et al.* (1996).

232. Amethyst-throated Sunangel

Heliangelus amethysticollis

French: Héliange à gorge améthyste

Spanish: Colibrí Gorgiamatista

German: Amethystsonnennympe

Taxonomy. *Ornismya amethysticollis* d'Orbigny and Lafresnaye, 1838. Yuracares, Cochabamba, Bolivia.

Forms a superspecies with *H. clarisse*, with which formerly considered conspecific; however, subtle morphological differences and markedly disjunct range support their treatment as separate species; *H. strophianus* may also belong in this superspecies. Three subspecies recognized.

Subspecies and Distribution.

H. a. laticlavus Salvin, 1891 - S Ecuador and N Peru.

H. a. decolor Zimmer, 1951 - E Andes in C Peru (S of R Marañón).

H. a. amethysticollis (d'Orbigny & Lafresnaye, 1838) - E Andes in S Peru and NW Bolivia.



Descriptive notes. 10 cm; 5.0-6.0 g. Male has blackish bill, straight, rather short; above shining dark green with a glittering green frontlet; underparts with throat and upper breast rosy amethyst, forming a glittering gorget; this is narrowly bordered on the neck and the sides of head by black and below by a cinnamon pectoral band; lower breast with glittering green discs, rest of underparts buff with green discs, especially on flanks; undertail-coverts beige; tail feathers bronze-green centrally and blue-black laterally, occasionally with whitish corners; tail rather short and only slightly forked. Female similar to male but throat rusty with some black flecks and often a few rose-coloured feathers. Immature similar to female. Race *laticlavus* differs in having a reddish-purple gorget, whitish breast band and buffy greyish belly; race *decolor* has frontlet lighter and greener, gorget deeper violet, breast band whiter, belly greyer, less buff.

Habitat. Wet and humid montane forests (cloudforest and dwarf and elfin forest) with abundant moss and epiphyte growth in subtropical and temperate zones. Also at forest edge, in bushy second

growth, and other open bushy terrain along streams up to humid grassy slopes. Mostly occurs in more or less closed woodland and is rather a cloudforest species. Seems to prefer damp bushy ravines and usually keeps inside the forest or close to the edges. Found at 1800-3200 m but most frequently observed above 2400 m.

Food and Feeding. Defends feeding territories over concentrated nectar resources, preferably centred on food plants with short corollas such as *Cavendishia*, *Palicourea* and *Aphelandra*. Can often be seen foraging in trees at low or middle strata (0.6-6 m), always near cover within or at the edge of forest. Often perches while feeding on small *Fuchsia* and *Brachyotum*; other food plants frequently visited are *Guzmania* and *Disterigma*. The species also has a high percentage of insects in the diet, which are hawked for in short sallies from low perches; sometimes observed amongst mixed flocks.

Breeding. May-Aug (Colombia) and Feb-Mar (Peru); nest is built of moss and other fine plant fibres about 1.5 m above ground; usually attached to a strand of moss hanging down from a branch and situated below an overhanging structure such as a clump of moss or a large leaf to gain protection from the weather. Clutch size 2; incubation by female; first breeding in second year. No further information.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Fairly common and sometimes even abundant. Protected by reserves in many areas throughout its extensive range, for instance in Cordillera Azul, Apurímac (Peru), and Beni (Bolivia).

Bibliography. Best *et al.* (1997), Bleiweiss (1992a, 1992b, 1994), Bloch *et al.* (1991), Bond & Meyer de Schauensee (1943), Brown & Bowers (1985), Butler (1979), Davies *et al.* (1994), Fjeldså & Krabbe (1990), Krabbe *et al.* (1997), Meyer de Schauensee (1982), Parker *et al.* (1982), Remsen (1985), Remsen & Traylor (1989), Snow & Snow (1980), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Wiedenfeld (1985), Williams & Tobias (1994), Zimmer (1951b).

233. Gorgeted Sunangel

Heliangelus strophianus

French: Héliange à queue bleue

Spanish: Colibrí Pectoral

German: Weißband-Sonnennympe

Taxonomy. *Trochilus* (—?) *strophianus* Gould, 1846, Ecuador.

Shares several characters with *H. clarisse* and *H. amethysticollis*, and may belong to same superspecies. "*H. violicollis*", known only from two skins of unknown origin, usually considered an aberrant form of present species, though this may not be the case. Other forms known mainly or exclusively from Bogotá trade skins include "*H. squamigularis*", "*H. barrali*" (from Antioquia), "*H. speciosus*", "*H. simoni*", "*H. rothschildi*", "*H. prosantis*" and "*H. luminosus*"; validity and possible affinities of these forms unknown. Monotypic.

Distribution. SW Colombia (Nariño) and NW Ecuador.



Descriptive notes. 10-11 cm; 5.3 g. Blackish bill short and straight. Male dark, almost velvety green above with a small glittering green frontlet; genus-typical gorget glittering rose-coloured to violet bordered by a white pectoral bar below, rest of underparts dark green, towards belly increasingly speckled with dark grey; forked tail dark steel blue. Female resembles male but has gorget reduced or absent, instead the throat region is dark grey-brown with most of the feathers fringed with white, occasionally with some glittering rosy feathers. Immature like female but the white pectoral band is usually narrower.

Habitat. Mainly humid and wet pre-montane forest but can also be found at shrubby forest borders and thickets. Records range from 1200 m up to (rarely) 2800 m. Most records are from subtropical zones but locally the species also occurs in temperate zones.

Food and Feeding. Usually seen alone, so probably territorial. In general seems to prefer damp bushy ravines. While foraging always stays near cover and rarely ventures into open areas. Mostly feeds at low flowers, less frequently visits flowers in the subcanopy region. No further information.

Breeding. Main season Oct-Dec; in SW Colombia, copulation recorded in Aug. Clutch size 2; incubation by female. No further information.

Movements. No information available but some seasonal vertical movements likely.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Chocó EBA. Fairly common in Pichincha (Ecuador) but populations may have declined substantially in recent times due to habitat destruction. In NW Ecuadorian part of range, species protected by Ecological Reserve Cotacachi-Cayapas. In SW Colombia, fairly common in Volcán Chiles area; protected in La Planada Reserve, where apparently rare.

Bibliography. Best, Clarke *et al.* (1993), Best, Heijnen & Williams (1997), Bleiweiss (1994), Bloch *et al.* (1991), Butler (1979), Fjeldså & Krabbe (1990), Hilty & Brown (1986), Kirwan & Marlow (1996), Meyer de Schauensee (1949, 1982), Ruschi (1964b), Salaman & Mazariegos (1998b), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Williams & Tobias (1994).

234. Tourmaline Sunangel

Heliangelus exortis

French: Héliange tourmaline

German: Grünband-Sonnennympe

Spanish: Colibrí Turmalina

Taxonomy. *Trochilus exortis* Fraser, 1840, Guaduas, Colombia.

Closely related to *H. micraster* and often regarded as conspecific. Coloration of throat region in female is subject to much variation; nevertheless, most patterns of variation appear irregular and not correlated with distribution, so no races can be determined. Monotypic.

Distribution. Andes of Colombia (all three ranges) and E slope of Andes in adjacent NW Ecuador. **Descriptive notes.** 10-11 cm; 4.0-4.6 g. Bill straight, medium-sized, blackish. Male dark shining green above with a narrow glittering green frontlet; below, chin is dark purple-blue, merging into the glittering rosy pink of the lower breast; gorget is bordered below by glittering emerald green; rest of underparts dusky grey with green discs, undertail-coverts white; tail is rather long, forked, central rectrices dark bronze, remaining ones blackish. Female resembles male, but lacks the glittering frontlet; chin blackish, throat whitish and speckled green to dusky, occasionally with some glittering rosy feathers; tail less forked. Immature like adult female, but chin of male white instead of blackish.



Habitat. Interior of humid and wet pre-montane forest and forest borders, most abundant in dense mossy cloudforest and elfin forests, often with some stands of bamboo. Frequently occurs at bushy clearings, hedges, and shrubby pastures from 1500 m to 3400 m, usually above 2300 m.

Food and Feeding. Territorial and rather aggressive. Forages rather low down in open or shrubby areas and forest borders, and can often be observed perching on top of bushes on the outer side of vegetation. Inside the forest mainly forages in lower strata. Flowers visited include *Salvia*, *Centropogon* and *Fuchsia*.

While feeding at flowers usually clings to them rather than hovering. Insects are caught by hawking and gleaned from surfaces of plants.

Breeding. Records suggest season in Mar-Aug. Courtship display has been observed in Jul. Clutch size 2; incubation by female.

Movements. Sedentary with occasional movements into upper tropical zone (Colombia).

Status and Conservation. Not globally threatened. CITES II. Locally fairly common. Occurs in several protected areas throughout its range such as Munchique National Park (Colombia) and North Podocarpus National Park (Ecuador). Many records from W Putumayo (SW Colombia).

Bibliography. Baez *et al.* (1997), Berlioz (1936b), Berlioz & Jouanin (1944), Best *et al.* (1997), Bleiweiss (1985a, 1985b, 1994), Bloch *et al.* (1991), Brown & Bowers (1985), Butler (1979), Fjeldsá & Krabbe (1990), Graves (1990), Greenway (1978), Hilty & Brown (1986), Jouanin (1950), Meyer de Schauensee (1949, 1982), Mobbs (1973b, 1973c), Poulsen (1996), Ridgely & Gaulin (1980), Schuchmann (1975a, 1983a), Stotz *et al.* (1996), Williams & Tobias (1994).

235. Little Sunangel

Heliangelus micraster

French: Héliange menu **German:** Goldkehl-Sonnennympe **Spanish:** Colibrí Lucero
Other common names: Gould's Sunangel

Taxonomy. *Heliangelus micraster* Gould, 1872, San Lucas, Ecuador.

Closely related to *H. exortis* and often regarded as conspecific. Two subspecies recognized.

Subspecies and Distribution.

H. m. micraster Gould, 1872 - E Andean slope of SE Ecuador and adjacent N Peru.

H. m. cutervensis Simon, 1921 - NW Peru (Cajamarca).



Descriptive notes. 10-11 cm; 3.6-4.1 g. Bill straight, blackish. Male upperparts dark metallic green with a glittering blue-green frontlet; dark metallic green below with a purplish-blue chin, grading into a highly iridescent yellow-orange gorget, bordered by a glittering emerald green; belly greyish, turning almost white towards vent, undertail-coverts white; tail forked, dark steel blue. Female has blackish chin and white throat, spotted with green to dusky grey discs and sometimes a few iridescent reddish-orange discs. Immature like female, young male lacking black chin. Race *cutervensis* has iridescent reddish-orange gorget.

Habitat. Dense mossy forest and forest borders; female frequently visits bushy pastures. Occurs in subtropical and temperate zones at elevations between 2300 and 3400 m; a few records are from altitudes as low as 1500 m.

Food and Feeding. Territorial; mainly forages low at forest borders or in open or shrubby areas. Inside the forest also keeps to lower and medium heights; sometimes can be seen perched on top of or on the outside of flowering bushes. Mainly feeds on nectar from flowers, sometimes clinging to them while feeding. Insects are caught in the air or gleaned from leaves.

Breeding. Jan-May in Ecuador. Clutch size 2; incubation by female. No further information available.

Movements. Sedentary; altitudinal dispersal after reproduction.

Status and Conservation. Not globally threatened. CITES II. Status not well known. Generally uncommon, though can be locally common, for instance in Loja (S Ecuador).

Bibliography. Best *et al.* (1997), Bleiweiss (1994), Fjeldsá & Krabbe (1990), Meyer de Schauensee (1982), Stotz *et al.* (1996), Zimmer (1951b).

236. Purple-throated Sunangel

Heliangelus viola

French: Héliange violette **German:** Purpurkehl-Sonnennympe **Spanish:** Colibrí Violeta

Taxonomy. *Heliotrypha viola* Gould, 1853, banks of River Marañón = Chachapoyas, Peru.

Relationships with congeners poorly known. Monotypic.

Distribution. W slope of Andes in S Ecuador and N Peru (S in W to Cajamarca, in E to Amazonas).

Descriptive notes. 11-12 cm; 5.1-6.6 g. Straight bill blackish. Male has shining green upperparts with a glittering blue-green frontlet; the highly iridescent gorget is deep violet and bordered below by a blue-green pectoral bar; belly green; the tail is rather long and deeply forked with the central pair of rectrices the same colour as the back, the outer tail feathers are blackish. Female similar to male but has no violet gorget, throat tawny to off-white, more or less speckled with bronzy green. Immature resembles female.



Habitat. Inhabits a wide range of habitats from cloudforest to shrubby thickets and *Alnus* woods. Found in subtropical and temperate zones at altitudes of 2150-3000 m.

Food and Feeding. The species has been recorded feeding at flowering *Eucalyptus* trees. In some areas of S Ecuador seems to be largely dependent on the introduced *Eucalyptus globulus*. Observations have shown that the species is closely correlated in its altitudinal distribution with the occurrence of that tree. Insects are caught in the air by hawking or are gleaned from the surface of leaves.

Breeding. Oct-Jan. Clutch size 2; incubation

by female. No further information.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Southern Central Andes EBA. Locally fairly common. In some areas apparently depends largely on the occurrence of introduced *Eucalyptus* trees for nectar. In Ecuador, present in several protected areas, e.g. Las Cajas National Recreation Area and North Podocarpus National Park.

Bibliography. Best & Clarke (1991), Best, Clarke *et al.* (1993), Best, Heijnen & Williams (1997), Bleiweiss (1994), Bloch *et al.* (1991), Brown & Bowers (1985), Butler (1979), Chapman (1926), Collar & Andrew (1988), Fjeldsá & Krabbe (1990), King (1989, 1991), Koepeke (1961), Meyer de Schauensee (1982), Parker *et al.* (1982), Ruschi (1961d, 1964b), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Williams & Tobias (1994), Zimmer (1951b).

237. Royal Sunangel

Heliangelus regalis

French: Héliange royal **German:** Blaue Sonnennympe **Spanish:** Colibrí Real

Taxonomy. *Heliangelus regalis* Fitzpatrick *et al.*, 1979, Cordillera del Cóndor, Peru.

This recently discovered species is distinguished from all other members of the genus by its almost entirely dark blue plumage and its deeply forked tail; female resembles those of several congeners, notably *H. mavors*; however, present species is apparently not closely related to any congener. Monotypic.

Distribution. N Peru on isolated Cordillera del Condor (Cajamarca) and E slope of Andes (San Martín).



Descriptive notes. 11-12 cm; 3.5-4.5 g. Bill short, straight, black. Male is entirely dark blue, slightly shining all over but with strongest iridescence on forehead; the long and deeply forked tail is also dark metallic blue. Female is dark green above, rich cinnamon below, spotted with bronzy green discs; the broad, pale buffy breast band resembles that of *H. mavors*; the tail is completely blue-black and not as forked as in male. Immature like female, but throat spotted grey rather than green; amount of blue in plumage increases steadily with age; typically, the blue gorget is acquired first.

Habitat. The species typically occurs in an unusual environment bordering several habitat types; it is most numerous in so-called "elfin scrub", a more xeric habitat consisting of grassland with mossy stunted forest with a canopy height of c. 4 m, stunted lichen-covered bushes, ericaceous plants, succulents and bracken ferns, adjacent to dry savanna-like areas on the one hand, and taller humid elfin forest on the other. This elfin scrub is located mainly on ridge tops and shows evidence of regular fire disturbance, preventing the development of taller forest. The species is also to be found along the sides of steep wooded ravines, but does not seem to inhabit deforested areas. Records range from 1350 to 2200 m in altitude, most abundant above 1500 m.

Food and Feeding. The main food plant seems to be *Brachyotum quinqueverve* (Melastomataceae), a low shrub with dark red tubular flowers. Males are highly territorial around stands of flowering bushes where they can be observed foraging within dense foliage mainly 0.5-2 m above ground. Territories have an estimated diameter of 40-50 m. While feeding, often perches rather than hovers; sometimes alights directly on the ground to feed from low flowers; the species has been observed extracting nectar through holes made by other birds, presumably flowerpiercers. Insects are gleaned from leaves or caught in the air by hawking.

Breeding. Only a few records exist, but these suggest a season of Jul-Sept. Clutch size 2; incubation by female. The species having been only recently discovered, no nest has yet been described.

Movements. No detailed studies have been carried out so far, but some seasonal vertical movements are most likely to occur; at times, males and females seem to prefer different elevations, females tending to occur lower down the slopes.

Status and Conservation. **VULNERABLE.** CITES II. Restricted-range species; present in Andean Ridge-top Forests EBA. Species is endemic to isolated mountain ranges of Peru near border with Ecuador. Range seems to be limited to a handful of sites; records are only numerous for the area around the type locality, e.g. San Cristóbal. Due to its restricted range and rather unusual habitat the species is sensitive to habitat fragmentation and destruction; its habitat is surrounded by cultivation; large areas have been deforested recently. Populations require monitoring; surveys required in order to try to locate other as yet undiscovered populations.

Bibliography. Bleiweiss (1994), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Davies *et al.* (1994, 1997), Davis (1986), Fitzpatrick *et al.* (1979), Fjeldsá & Krabbe (1990), Graves (1993), Hinkelmann (1987), Parker *et al.* (1982), Seddon *et al.* (1996), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Vuilleumier & Mayr (1987), Wege & Long (1995).



PLATE 67

inches 2
cm 5

Genus *ERIOCNEMIS* Reichenbach, 1849

238. Black-breasted Puffleg

Eriocnemis nigrivestis

French: Ériane à robe noire

Spanish: Calzadito Pechinegro

German: Schwarzbauch-Höschekolibri

Taxonomy. *Trochilus nigrivestis* Bourcier and Mulsant, 1852, Tumbaco, Ecuador.

Closely related to *E. vestitus* and *E. derbyi*. Doubtful species "*E. soederstroemi*" is regarded by some authors as a hybrid of present species and *E. luciani*, or a race or aberrant form of *E. godini*. Monotypic.

Distribution. NW Ecuador, mainly on volcanoes Pichincha and Atacazo, but also known from Imbabura; recent records only from ridge crests of Frutillas, Yanacocha, Cerro Alaspungo and Cerro Pugi.



Descriptive notes. 8-9 cm; 4.3-4.6 g. Male has straight, black bill; upperparts entirely blackish with only a faint green sheen in certain lights; uppertail-coverts shining dark blue; underparts also blackish with glittering violet-blue throat patch and undertail-coverts; tail dark steely blue and moderately forked; leg puffs white. Female shining bronze-green above grading into bluish-green on rump and uppertail-coverts; below golden green with light blue gular patch; tail, undertail-coverts and leg puffs as in male; resembles female *E. vestitus*, but below more golden green instead of cinnamon; belly with whitish fringes;

uppertail-coverts more bluish and less strongly glittering than in *E. vestitus*. Immature resembles adult female but head feathers with buff fringes.

Habitat. Confined to crests of ridges on mountains around Quito, the species appears to depend on certain type of habitat found exclusively on flat tops of these ridges bordering páramo: this habitat is characterized by shorter and denser vegetation than in neighbouring areas; typically consists of stunted elfin forest, with an average canopy height of 8-10 m and a dense undergrowth of many ericads and epiphytes, the forest being locally interrupted by grassy clearings and second growth with brambles (*Rubus*). Occurs in temperate zones; records range from 2400 to 4600 m in elevation, but are most numerous at 2745-3050 m in Apr-Jun and 3100-4570 m in Nov-Feb, suggesting some seasonal altitudinal movements dependent on plant flowering. Outside breeding season, males are typically observed at higher altitudes than females.

Food and Feeding. Territorial. Prefers flowers of *Palicourea huigrensis*, a small rubiad tree with bright blue flowers; also feeds on nectar from a variety of shrubs, herbs and vines, mostly below 2 m in dense vegetation. Many ericads, for example *Thiboudia floribunda*, *Macleania macrantha* and *Disterigma*, but also *Rubus*, *Tropaolum*, *Psychotria* and *Miconia* have been recorded as food plants. Typically feeds from plants with straight tubular flowers, hovering but also frequently perched or alighting directly on the ground. Insects are obtained mostly by flycatching. The species has been observed feeding from holes at corolla base, made either by them or, more likely, by the Glossy Flowerpiercer (*Diglossa lafresnayii*).

Breeding. Oct-Mar. Clutch size 2; incubation by female. No further information available.

Movements. Records suggest occurrence at higher elevations outside breeding season; see Habitat. **Status and Conservation.** CRITICALLY ENDANGERED. CITES II. Restricted-range species: present in Central Andean Páramo EBA. Rare and local, and apparently close to extinction. Numerous specimens in museum collections suggest that species might have been fairly common in past, but only a few recent records exist. The species is endemic to a small area covering the slopes of two adjacent volcanoes, Pichincha and Atacazo, with a few additional records from Imbabura. It is confined to habitats characterized by a certain type of vegetation: the species typically occurs on top of ridge crests dominated by stunted elfin forest with a high percentage of epiphytes and ericads. Decrease in population size is probably due to destruction of this habitat; the natural vegetation of these ridges has largely been removed to create cultivation and pastures for cattle and for charcoal burning. Recently, species has also been recorded on Cerro Pugi, but deforestation is rapidly proceeding there too. Charcoal production on the slopes of Pichincha, just outside Quito, is now prohibited, and access to the area is controlled; the creation of a reserve has been proposed.

Bibliography. Best *et al.* (1997), Bleiweiss (1982), Bleiweiss & Olalla (1983), Butler, A. L. (1926c), Butler, T. Y. (1979), Chapman (1926), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Fjeldså & Krabbe (1990), Graves (1996), Knox & Walters (1994), Krabbe *et al.* (1994), Lyons (1997), Meyer de Schauensee (1982), Oberholser (1902), Paynter & Traylor (1977), Phillips (1998), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Taylor (1995), Wege & Long (1995).

239. Glowing Puffleg

Eriocnemis vestitus

French: Ériane pattue

German: Violettekehl-Höschekolibri

Spanish: Calzadito Reluciente

Taxonomy. *Ornismya vestita* Lesson, 1838, Bogotá, Colombia.

Closely related to *E. nigrivestis* and *E. derbyi*. Race *paramillo* isolated in range from the other populations and morphologically fairly distinct; differences slighter between nominate and race *smaragdinipectus*. Three subspecies recognized.

Subspecies and Distribution.

E. v. paramillo (Chapman, 1917) - N parts of W & C Andes of Colombia.

E. v. vestitus (Lesson, 1838) - NW Venezuela and E Andes of Colombia.

E. v. smaragdinipectus Gould, 1868 - SW Colombia and Andes of Ecuador and extreme N Peru.

Descriptive notes. 9-10 cm; 4.4-5.2 g. Bill straight, blackish. Male shining dark green above, becoming golden green on rump and uppertail-coverts; throat and upper breast are shining blackish-



green, belly glittering golden green; a conspicuous character is the glittering purple throat patch surrounded by a narrow golden green fringe; the undertail-coverts show a strongly iridescent purplish-blue, the large downy leg puffs are white, contrasting with the forked and dark steel blue tail. Female has upperparts shining golden green; below cinnamon-buff malar stripe, throat and breast buff spotted with glittering golden green discs; the greyish-white belly also has green discs; throat patch is reduced to a few bluish-purple discs. Immature similar to female. Race *paramillo* lacks golden green fringe to throat patch; male of race

smaragdinipectus tends to have a broader throat patch than those of other races.

Habitat. Favours fairly open habitats in temperate and páramo zones and primarily inhabits upper montane forest borders in cloudforest and dwarf forest, but also bushy slopes, overgrown pastures and humid páramo with heather-like shrubs such as *Pernettya* and *Hypericum*. Occasionally found in more densely wooded areas in subtropical zone. The species has been recorded at altitudes of 2250-3850 m, with most records at 2800-3500 m.

Food and Feeding. Pugnacious and territorial around food plants with short corolla tubes, such as *Palicourea*. Usually at low flowers on the outside of shrubbery, or flowers of low ericads and rubiads, and also recorded visiting *Tillandsia* blooms. While visiting flowers, hovers, perches, or sometimes clings to flowers. Insects are caught by hawking.

Breeding. Breeding records are from late Jun (Antioquia) and Dec (S Colombia). The nest is often built in grass stands. Clutch size 2; incubation by female; first breeding in second year. No further information.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Fairly common throughout range. Readily accepts secondary growth and overgrown pastures. Common in Puracé National Park (Colombia); also occurs in Pasochoa Forest Reserve and North Podocarpus National Park (Ecuador).

Bibliography. Best *et al.* (1997), Bloch *et al.* (1991), Brown & Bowers (1985), Butler (1979), Chapman (1917), Fjeldså & Krabbe (1990), Hartert (1922), Hilty & Brown (1986), King (1991), Meyer de Schauensee (1949), Meyer de Schauensee & Phelps (1978), Mobbs (1974), Parker *et al.* (1985), Snow & Snow (1980), Stotz *et al.* (1996), Williams & Tobias (1994), Zimmer (1951b).

240. Black-thighed Puffleg

Eriocnemis derbyi

French: Ériane de Derby

German: Schwarzfeder-Höschekolibri

Spanish: Calzadito Patinegro

Taxonomy. *Trochilus Derbyi* DeLatre and Bourcier, 1846, Vólcan de Puracé, near Popayán, Colombia.

Closely related to *E. nigrivestis* and *E. vestitus*. Populations at northern end of range have a slightly longer bill; these were formerly regarded as race *longirostris*, but variation is clinal. Monotypic.

Distribution. C Andes of Colombia and NW Ecuador.



Descriptive notes. 10 cm. Bill straight, blackish. Male shining golden green above and below, underparts appearing black in certain lights; uppertail- and undertail-coverts are strongly glittering malachite green, contrasting with the black leg puffs; tail forked and pointed, black. Female and immature are similar but with underparts more white thickly spotted with glittering green discs and with leg puffs mixed black and greyish-white. Female shows a blue line on forehead. Immature similar to female.

Habitat. Inhabits humid forest borders and bushy pastures; in addition there are records from shrubby ravines above Puracé (Colombia). In general the species seems to prefer fairly open vegetation at elevations of 2500-3600 m, commonest above 2900 m.

Food and Feeding. Territorial; takes nectar of low-growing flowers such as *Fuchsia* and *Ericaceae*. Insects are caught by hawking.

Breeding. Records from Puracé suggest season in Feb. Clutch size 2; incubation by female; first breeding in second year. No further information.

Movements. Sedentary with seasonal altitudinal movements.

Status and Conservation. Not globally threatened. CITES II. Currently considered Near-threatened. Restricted-range species: present in Northern Central Andes EBA. Generally uncommon to locally common. Readily takes to man-made habitats like pastures and gardens, but populations require monitoring. Occurs in Puracé National Park (Colombia).

Bibliography. Best *et al.* (1997), Butler (1979), Chapman (1917, 1926), Collar & Andrew (1988), Fjeldså & Krabbe (1990), Hilty & Brown (1986), Meyer de Schauensee (1949, 1982), Renjifo *et al.* (1997), Salaman & Mazariegos (1998b), Stattersfield *et al.* (1998), Stotz *et al.* (1996).

241. Turquoise-throated Puffleg

Eriocnemis godini

French: Ériane turquoise

German: Türkiskehl-Höschekolibri

Spanish: Calzadito Turquesa

Taxonomy. *Trochilus Godini* Bourcier, 1851, Guayabamba, Ecuador.

Forms superspecies with *E. cupreiventris*. Doubtful species "*E. soederstroemi*" is regarded by some authors as a race or aberrant form of present species, or a hybrid of *E. nigrivestis* x *E. luciani*. Monotypic.

Distribution. NW Ecuador; possibly also SW Colombia.



Descriptive notes. 10-11 cm. Male has straight, black bill; upperparts shining golden green turning to bluish-green on rump and uppertail-coverts; glittering green below with diffused faint blue throat patch and golden sheen on belly, undertail-coverts glittering violet; tail blue-black and slightly forked; leg puffs white. Female similar to male but lacks iridescent throat patch; plumage in general less strongly glittering and more golden on belly. Immature plumage unknown, but probably similar to that of female.

Habitat. The species has been recorded from ravines in Guallabamba and Tungurahua in NW

Ecuador at elevations between 2100 and 2300 m where it inhabits forests and shrubby forest edge.

Food and Feeding. Feeding habits poorly known; mainly feeds on nectar but no information concerning preferred food plants available; amount of insects taken uncertain.

Breeding. Clutch size 2; incubation by female. No further information available, but habits probably similar to those of congeners.

Movements. Probably sedentary.

Status and Conservation. CRITICALLY ENDANGERED. CITES II. Restricted-range species: present in Chocó EBA. Little known and might even be extinct. Evidence of species amounts to a few old records from NW Ecuador and specimens from Bogotá collections probably obtained in SW Colombia; the species has not been recorded during present century apart from one unconfirmed sighting from Chillo Valley near Quito. Due to lack of data, habitat requirements are hardly known; however, records suggest occurrence in steep and possibly arid valleys. The species occurs in very a small range, within which the natural vegetation has probably now been destroyed almost entirely; only in a few places can remnants of apparently natural habitat still be found in steep ravines on upper R Guallabamba, as well as around Palalahuia and on R Blanco. As the exact distribution of the species is uncertain, it is possible that it still exists in small numbers in secluded areas and has been overlooked due to inaccessibility of its habitat. The area around the type locality where the species is most likely to occur is not within a protected area.

Bibliography. Berlioz (1971a), Best *et al.* (1997), Butler (1979), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Fjeldså & Krabbe (1990), Graves (1996), Hilty (1985), Hilty & Brown (1986), Knox & Walters (1994), Paynter & Traylor (1977, 1981), Renjifo *et al.* (1997), Salaman & Mazariegos (1998b), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Wege & Long (1995).

242. Coppery-bellied Puffleg

Eriocnemis cupreiventris

French: Érione à ventre cuivré

Spanish: Calzadito Cobrizo

German: Kupferbauch-Höschchenkolibri

Taxonomy. *Trochilus cupreus-ventris* Fraser, 1840, Bogotá, Colombia.

Forms superspecies with *E. godini*. Monotypic.

Distribution. NW Venezuela (Andes of Mérida) and E Andes of Colombia.



Descriptive notes. 9-10 cm; averages 5-6 g. Bill straight, black. Male shining green above, turning bluish-green on uppertail-coverts; underparts glittering green, becoming golden copper on centre of belly; undertail-coverts are glittering violet, contrasting with forked blue-black tail and white downy leg puffs. Sexes similar, but female has greyish-white speckled throat and less coppery underparts. Immature has breast blackish, belly lacks the coppery hue.

Habitat. Prefers open vegetation such as montane forest borders, low shrubby slopes and open páramo, at times also inside humid

forest. Generally to be found in upper subtropical and lower temperate zones, but sometimes ascending to páramo altitude. Occurs at 2000-3000 m, most abundant above 2500 m.

Food and Feeding. Pugnacious and territorial around small flowering trees and shrubs. Food plants with short corollas, such as *Palicourea*, *Cavendishia* and *Pernettya*, are preferred. While feeding clings to flowers. Hawks for insects from perches.

Breeding. Sept-Jan. The large nest is often situated in dense vegetation. Clutch size 2; incubation by female. First breeding in second year. No further information.

Movements. Sedentary with altitudinal dispersal.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Cordillera de Mérida EBA and Colombian East Andes EBA. Locally fairly common; although there are many records from Cundinamarca (Colombia) and Mérida (Venezuela) at the extremes of the range, only a few observations have been made for the intervening regions.

Bibliography. Fjeldså & Krabbe (1990), Hilty & Brown (1986), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Mobbs (1974), Snow & Snow (1980), Stattersfield *et al.* (1998), Stotz *et al.* (1996).

243. Sapphire-vented Puffleg

Eriocnemis luciani

French: Érione catherine

Spanish: Calzadito Colilargo Norteño

German: Langschwanz-Höschchenkolibri

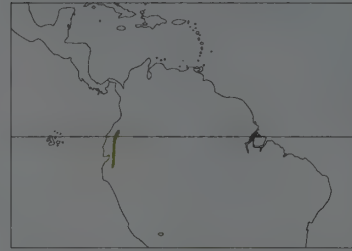
Other common names: Long-tailed Puffleg

Taxonomy. *Trochilus luciani* Bourcier, 1847, Guaca, Ecuador.

Often considered conspecific with *E. sapphiropygia*, and intermediate specimens exist, but morphological differences support treatment as separate species. Doubtful species "*E. soederstroemi*" is regarded by some authors as a hybrid of present species and *E. nigrirostris*, or a race or aberrant form of *E. godini*. "*E. isaacsonii*", known only from three Bogotá trade skins which are not identical, may be a hybrid of undetermined species of *Eriocnemis* x *Helianthus*. Monotypic.

Distribution. Andes of SW Colombia (Nariño) and W Ecuador.

Descriptive notes. 12-5-14 cm (including long tail); 5-4-6-4 g. Bill straight, black. Male has upperparts metallic grass green with shining dark blue forecrown; glittering golden green below,



undertail-coverts glittering purple; the downy leg puffs are white; tail long and deeply forked, blue-black. Sexes similar, but female has shorter wings and a less deeply forked tail; in addition, lacks the white basal parts of throat feathers present in male, but this character is only visible in the hand. Immature probably similar to female.

Habitat. Prefers fairly open vegetation like edges and glades of wet montane forest and bushy and grassy páramo slopes. Found in temperate zones mainly at elevations between 2800 and 4800 m.

Food and Feeding. Territorial and pugnacious. Usually seen feeding on low-growing flowers at vegetation borders and on open grassy slopes. Often alights directly on the ground when feeding from small terrestrial flowers. Food plants recorded are *Embothrium*, mistletoes, *Bomarea* and *Siphocampylus*. Hawks for small arthropods in the air.

Breeding. Few records available but probably Feb-Mar. The cup-shaped nest consists mainly of moss, lichen and pieces of fern leaves held together by spider webs; usually attached to one side of a thin twig or root. Nest-sites on overgrown slopes are preferred to give the nest protection from weather and predation. Clutch size 2; incubation by female. First breeding in second year. No further information.

Movements. Sedentary but vertical seasonal movements likely.

Status and Conservation. Not globally threatened. CITES II. Locally very common, especially in the vicinity of Mt Pichincha; also occurs in several protected areas such as Pascocha Forest Reserve and Las Cajas National Recreation Area (Ecuador).

Bibliography. Best *et al.* (1997), Bloch *et al.* (1991), Brown & Bowers (1985), Butler, A.L. (1926c), Butler, T.Y. (1979), Fjeldså & Krabbe (1990), Graves (1996), Hilty & Brown (1986), King (1991), Meyer de Schauensee (1982), Mobbs (1974), Rutgers & Norris (1972), Schuchmann (1988), Stotz *et al.* (1996), Zimmer (1951b).

244. Coppery-naped Puffleg

Eriocnemis sapphiropygia

French: Érione à ventre bleu

Spanish: Calzadito Colilargo Sureño

German: Kupfernacken-Höschchenkolibri

Taxonomy. *Eriocnemis sapphiropygia* [sic] Taczanowski, 1874, Maraynioc, Peru.

Often considered conspecific with *E. luciani*, and intermediate specimens exist, but morphological differences support treatment as separate species. Racial distributions in NC Peru not well known, and they intergrade in E La Libertad. Possible race *marcapatae* (SE Peru) barely differs from nominate. Two subspecies currently recognized.

Subspecies and Distribution.

E. s. catharina Salvin, 1897 - E Andes of N Peru (Ucubamba Valley).

E. s. sapphiropygia Taczanowski, 1874 - E Andes of C & S Peru (Pasco and Junín to Puno).

Descriptive notes. 11-12 cm; 5-5-6-0 g. Bill straight, blackish. Male glittering metallic grass green above, with a golden coppery tinge on back of head and neck; underparts more golden green, undertail-coverts are shining purplish-blue; tail forked, steel blue; the rather large leg puffs are white. Sexes similar, but female has white subterminal band on throat feathers, giving the throat a speckled appearance; central belly with white stripe. Immature probably similar to female. Male of race *catharina* differs in slightly bluish forehead and dark blue sheen on belly; female has bluish tinge on belly.



Habitat. Mainly inhabits edges and glades of wet montane forest in subtropical zone, but also on bushy slopes. Records range from 2000 to 4000 m in altitude, but most are from 2600-3500 m.

Food and Feeding. Pugnacious and territorial at clusters of flowers. Nectar is taken from a wide variety of food plants, low at vegetation borders. Often clings to flowers rather than hovering in front of them. Feeding habits in general are much like in *E. luciani*.

Breeding. Clutch size 2; incubation by female. No further information available.

Movements. No information, but some seasonal altitudinal movements likely.

Status and Conservation. Not globally threatened. CITES II. Reported to be locally common. Biology and ecology not well known, and taxonomy uncertain; research required.

Bibliography. Fjeldså & Krabbe (1990), Meyer de Schauensee (1982), Zimmer (1951b).

245. Golden-breasted Puffleg

Eriocnemis mosquera

French: Érione à poitrine d'or

Spanish: Calzadito de Mosquera

German: Goldbrust-Höschchenkolibri

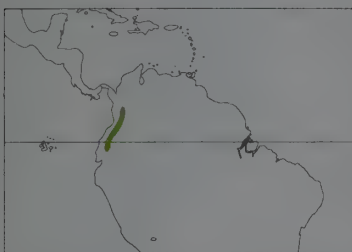
Taxonomy. *Trochilus Mosquera* DeLattre and Bourcier, 1846, Pasto, Colombia.

Birds from N part of C Cordillera of Colombia are slightly greener in overall coloration and have a longer bill; these were formerly awarded race *bogotensis*, but as variation is clinal subspecific rank is not appropriate. Monotypic.

Distribution. SW & C Andes of Colombia (S from Caldas) to NW Ecuador. Contrary to previous reports, does not occur in E Andes of Colombia.

Descriptive notes. 12-13 cm; 5-2-5-8 g. Male has straight, black bill; shining green above, more bronze-green on neck and rump; underparts glittering golden green, lower throat and upper breast coppery bronze, undertail-coverts dull brownish with metallic green tips on those closest to vent; tail long and deeply forked, with the central pair of feathers blue-green, the rest dark green to almost blue-black in the outer two pairs; leg puffs white; male has white basal parts to throat feathers (not visible in field). Female similar to male but with shorter wings and tail; undertail-coverts slightly greener. Immature probably similar to female.

Habitat. Mainly inhabits elfin forest and stunted montane woodland, but can also be found at forest borders, bushy clearings and thickets near tree-line. Occurs between 1200 and 3600 m, com-



monest at 2900-3300 m; generally in temperate zone but occasionally and seasonally down to tropical habitats.

Food and Feeding. Males are territorial and aggressive as are all members of the genus. Typically feeds at low flowers on the outside of dense bushes in elfin woodland and shrubby clearings; while feeding may hover or briefly cling to flowers.

Breeding. Breeding activity recorded in Nov (Colombia). The cup-shaped nest is built of moss and small sticks held together by spider webs and lined with fine plant material; it is typically attached to a branch or strand of moss

forming a hanging construction and situated below a rock overhang or similar structure providing protection from rain. Clutch size 2; incubation by female. No further information.

Movements. Some seasonal altitudinal movements down to upper tropical zone at c. 1000-1500 m. **Status and Conservation.** Not globally threatened. CITES II. Throughout its range the species is protected in several reserves along the C Andes of Colombia and NW Ecuador, common in Puracé National Park (Colombia), and around Mt Pichincha (Ecuador); also occurs in Paschoa Forest Reserve (Ecuador).

Bibliography. Best *et al.* (1997), Bleiweiss (1988a), Brown & Bowers (1985), Butler (1979), Fjeldsá & Krabbe (1990), Hilty (1994), Hilty & Brown (1986), Meyer de Schauensee (1982), Olrog (1968), Salaman & Mazariegos (1998b), Stotz *et al.* (1996), Tye & Tye (1990), Vélez & Velázquez (1998).

246. Blue-capped Puffleg

Eriocnemis glaucopoides

French: Ériane à front bleu **German:** Blaustirn-Hörschenkolibri **Spanish:** Calzadito Frentiazul

Taxonomy. *Ornismya glaucopoides* d'Orbigny and Lafresnaye, 1838, Valle Grande, Bolivia. This southernmost of pufflegs has no obvious close relative; possibly nearest to *E. alinae*. Monotypic. **Distribution.** C & SE Bolivia and NW Argentina.



Descriptive notes. 9-10 cm; 4.0-4.5 g. Bill straight, black; the downy white leg puffs are not as large as in congeners. Male dark green above with strongly glittering blue forehead; underparts golden green, becoming bluish-green on the lower breast, undertail-coverts are shining purplish-blue; tail long, blue-black. Female has underparts brightly cinnamon-buff, and green discs on sides and vent. Immature male lacks glittering blue on forehead.

Habitat. Temperate zones at elevations of 1500-2900 m; records are most frequent between 2000 and 2500 m. Preferred habitat is humid slopes covered with grass and dense

shrubby, and the edges of cloudforest. In Argentina sometimes also in less humid habitats dominated by Myrtaceae and stunted trees.

Food and Feeding. The species has been observed feeding at flowers low down at vegetation borders.

Breeding. At Cochabamba (Bolivia) breeding recorded Nov, juvenile males have been observed Dec and Feb. Clutch size 2; incubation by female. First breeding in second year. No further information.

Movements. Sedentary, but altitudinal movements during wet and dry seasons in NW Argentina. **Status and Conservation.** Not globally threatened. CITES II. Restricted-range species; present in Argentine and South Bolivian Yungas EBA. Generally considered to be rare to locally common. Present in Calilegua National Park, Argentina.

Bibliography. Babarskas *et al.* (1995), Berlioz (1971a), Blake & Rougès (1997), Blendinger (1998), Bond & Meyer de Schauensee (1943), Canevari *et al.* (1991), Fjeldsá & Krabbe (1990), Fjeldsá & Mayer (1996), Krabbe *et al.* (1996), Meyer de Schauensee (1982), Narosky & Yzurieta (1993), Olrog (1984), de la Peña (1994), Remsen & Traylor (1989), Remsen, Traylor & Parkes (1986), Stattersfield *et al.* (1998), Stotz *et al.* (1996).

247. Colorful Puffleg

Eriocnemis mirabilis

French: Ériane multicolore **German:** Blaubauch-Hörschenkolibri **Spanish:** Calzadito Admirable

Taxonomy. *Eriocnemis mirabilis* Meyer de Schauensee, 1967, Charguayaco, 2200 m, Cauca, Colombia.

Forms a superspecies with *E. alinae*, from which it is separated by the arid valley of R Patia. Monotypic.

Distribution. W slope of W Andes of Colombia (Cauca).



Descriptive notes. 8-9 cm. Bill straight, blackish; feet pink; the very large leg puffs are white with cinnamon tips in both sexes. Male dark shining green above with a glittering emerald green frontlet; underparts very colourful with an iridescent green gorget, glittering indigo blue belly, and glittering red and coppery undertail-coverts; tail forked, dark bronzy-green, under surface of rectrices strongly shining golden bronzy-green. Female mainly white below, with green discs on sides of throat and breast, and reddish-bronze discs on flanks and sides of belly. Immature probably similar to female.

Habitat. Wet forest and forest borders in subtropical zones at elevations of 2200-2440 m. Undisturbed cloudforest is preferred, but the species has also been observed at forest edges and small clearings. The habitat is characterized mainly by *Billia colombiana*, *Clusia*, *Persea*, *Hyeronima colombiana*, *Quercus humboldtii* and *Weinmannia pubescens*.

Food and Feeding. Feeds at flowers of *Miconia* and *Clusia*, among others, at heights of 2-4 m above ground.

Breeding. Since this species was discovered only recently, breeding remains unobserved.

Movements. Sedentary.

Status and Conservation. **VULNERABLE.** CITES II. Restricted-range species; present in Chocó EBA. To date this species is only known from the area around the type locality, and it is probably endemic to that region. Despite some recent deforestation in the vicinity the area seems to be facing comparatively little disturbance for the present and in the near future; the construction of a new road might pose a potential threat from human interference. The only known locality for the present species lies within the Munchique National Park, and close to the recently established Los Tambitos Nature Reserve, where it might also occur. For an accurate assessment of its present conservation status, more data required on the exact range and ecological requirements of the species.

Bibliography. Berlioz (1971a), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Fjeldsá & Krabbe (1990), Hilty (1985), Hilty & Brown (1986), Hinkelmann (1987), Mayr & Vuilleumier (1983), Meyer de Schauensee (1967, 1982), Negret (1991), Renjifo *et al.* (1997), Salaman & Mazariegos (1998a), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Wege & Long (1995).

248. Emerald-bellied Puffleg

Eriocnemis alinae

French: Ériane d'Aline **German:** Weißbrust-Hörschenkolibri **Spanish:** Calzadito Pechiblanco

Taxonomy. *Ornismya Alinae* Bourcier, 1842, Tunja, Colombia.

Forms a superspecies with *E. mirabilis*, from which it is separated by the arid valley of R Patia. Two subspecies recognized.

Subspecies and Distribution.

E. a. alinae (Bourcier, 1842) - SC & E Andes of Colombia to E Andes of Ecuador.

E. a. dybowskii Taczanowski, 1882 - E Andes of N & C Peru.



Descriptive notes. 8-9 cm; 4.0-4.5 g. Bill black, straight; very large downy white leg puffs. Male upperparts dark shining green with a narrow, glittering bluish-green frontlet; underparts also glittering bluish-green with a large white patch on central breast, more or less spotted with green discs; the rather short and slightly forked tail is green and stronger iridescent on its under surface. Sexes similar, but female lacks glittering frontlet and tends to have shorter wings and tail. Immature probably similar to female. Race *dybowskii* distinctly larger and has glittering frontlet much reduced; in addition, the white breast patch is less sharply defined.

Habitat. Wet montane forests of tropical and subtropical zones; prefers humid vegetation like cloudforests, where frequently seen in small glades. Less often found at forest edges and rather avoids more open habitats. Usually recorded at altitudes of 2300-2800 m.

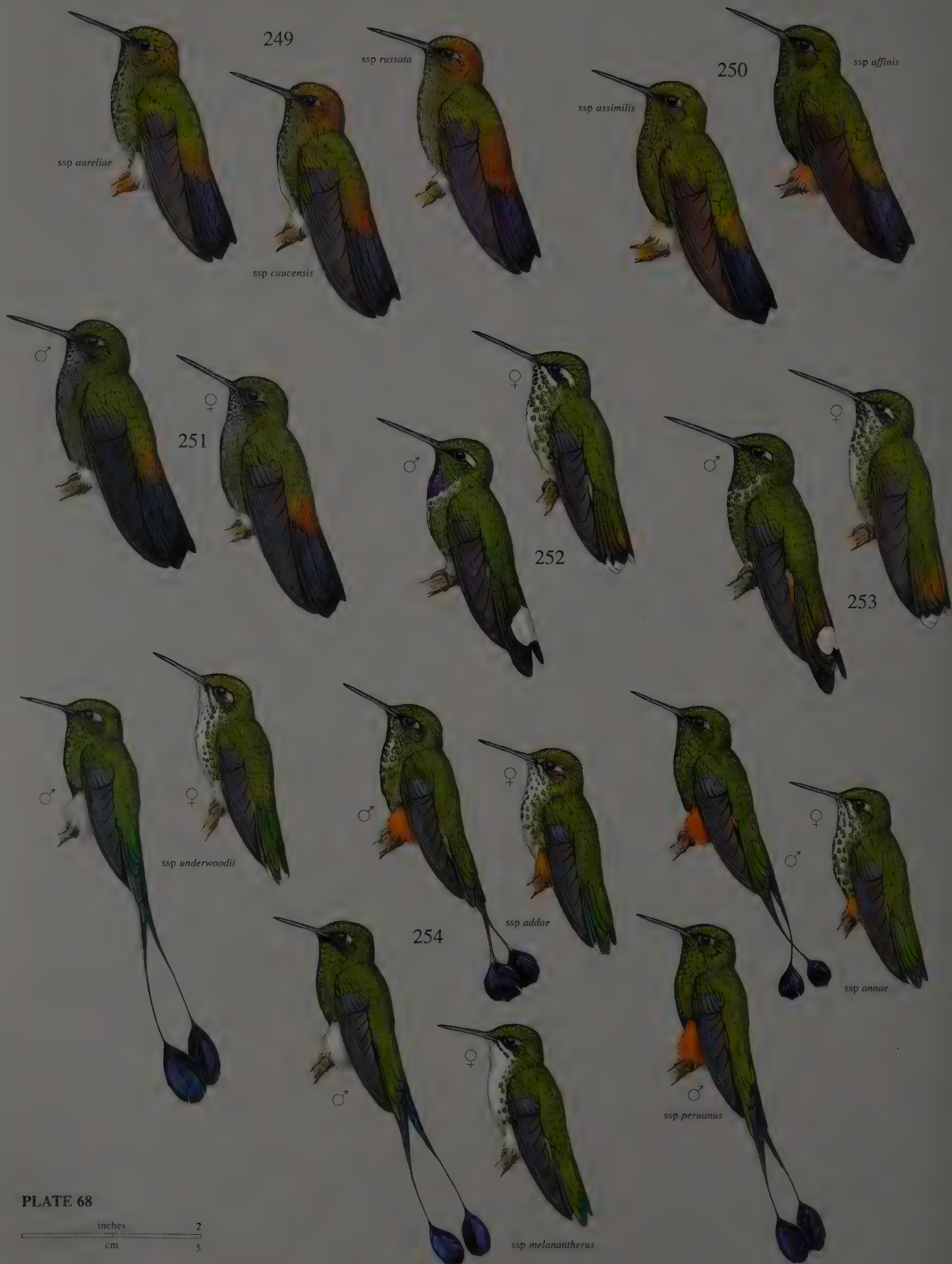
Food and Feeding. Mainly takes nectar from flowers at 1-3 m above ground inside dense vegetation. Small insects are an additional food source.

Breeding. Nest undescribed; no information on breeding season.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Distribution rather local; one reason for this might be habitat loss, since the species seems to depend on humid forests which have already suffered heavy damage, and are currently under threat of further deforestation.

Bibliography. Berlioz (1959, 1971a), Best *et al.* (1997), Butler (1979), Davies *et al.* (1994), Fjeldsá & Krabbe (1990), Hilty (1985), Hilty & Brown (1986), Meyer de Schauensee (1949, 1982), Olrog (1968), Salaman & Mazariegos (1998a, 1998b), Stotz *et al.* (1996), Zimmer (1951b).



Genus *HAPLOPHAEDIA* Simon, 1918

249. Greenish Puffleg

Haplophaedia aureliae

French: Ériane d'Aurélié

German: Kupferglanz-Hörschenkolibri

Spanish: Calzadito Verdoso Norteño

Taxonomy. *Trochilus Aureliae* Bourcier and Mulsant, 1846, Bogotá, Colombia.

Genus sometimes merged into *Eriocnemis*; also considered to be close to *Urosticte* and *Ocreatus*. May form superspecies with *H. assimilis*; these two usually considered conspecific, but plumage differences, together with disjunct distributions, support their treatment as separate species. Throughout its range this species shows considerable variation and consequently several additional races have been proposed: *galindoi* and *floccus*, both from Darién, included within *caucensis*; and *bernali*, from Santander (NC Colombia), within nominate. Three subspecies currently recognized.

Subspecies and Distribution.

H. a. caucensis (Simon, 1911) - SE Panama and W & C Andes of Colombia.

H. a. aureliae (Bourcier & Mulsant, 1846) - E Andes of Colombia, and probably also E slope of C Andes.

H. a. russata (Gould, 1871) - E slope of Andes of Ecuador.

Descriptive notes. 9-10 cm; male and female 4.7-6.5 g. Bill straight, blackish. Male green above with a coppery hue, especially on head and neck; underparts are duller green, feathers fringed greyish-white; large, conspicuous leg puffs are white on the outside, buffy on the inside; tail slightly forked, blue-black. Sexes similar but female appears more heavily scaled below, and has leg puffs all white. Immature resembles female. Race *caucensis* has upperparts more grass-green, with more coppery tinge to head and rump, and more extensive white below, forming a white patch on central belly; *russata* differs in having a longer bill,



even more and brighter coppery areas on upperparts, and almost completely lacking the white parts below, the feathers being fringed brownish instead.

Habitat. The species inhabits the understorey of humid and wet montane and pre-montane forest and forest borders in subtropical zones at altitudes of 1500-3100 m; most abundant below 2500 m.

Food and Feeding. Territorial and pugnacious. Feeding territories are established around flowers with short corollas. The species is usually found in the lower storey of the forest interior, occurring in canopy only when *Inga* trees are in flower. Gleans insects from leaves.

Breeding. Dec-Mar, but nesting has also been recorded May-Aug, and in Sept. The cup-shaped nest consists mainly of moss held together with cobwebs and lined with fine plant material. It is usually built beneath a fern or *Heliconia* leaf to provide protection from rain. Usually placed 0.5-2 m above ground. Clutch size 2; incubation by female. First breeding in second year. No further information.

Movements. Records from Colombia suggest some seasonal altitudinal movements to lower temperate zone.

Status and Conservation. Not globally threatened. CITES II. Generally fairly common, and locally even abundant. In SW Colombia, above Cali, recorded densities of at least 3-5 pairs/km². Regularly recorded between Tena and Coca, NE Ecuador.

Bibliography. Bertioz (1936b), Bertioz & Jouanin (1944), Best *et al.* (1997), Brown & Bowers (1985), Butler (1979), Chapman (1917), Davies *et al.* (1994), Fjeldså & Krabbe (1986, 1990), Greenway (1978), Hilty (1997), Hilty & Brown (1986), Jouanin (1950), Meyer de Schauensee (1949, 1982), Miller (1963), Ridgely & Gaulin (1980), Ridgely & Gwynne (1989), Romero & Hernández (1979), Schuchmann (1979a, 1990a), Stotz *et al.* (1996), Wetmore (1968a).

250. Buff-thighed Puffleg

Haplophaedia assimilis

French: Ériane à pattes rouges

German: Fahlschenkel-Hörschenkolibri

Spanish: Calzadito Verdoso Sureño

Taxonomy. *Eriocnemis assimilis* Elliot, 1876, Apolo and Tilitilo, La Paz, Bolivia.

Genus sometimes merged into *Eriocnemis*; also considered to be close to *Urosticte* and *Ocreatus*. May form superspecies with *H. aureliae*; these two usually considered conspecific, but plumage differences, together with disjunct distributions, support their treatment as separate species. Two subspecies recognized.

Subspecies and Distribution.

H. a. affinis (Taczanowski, 1884) - E Andes of N & C Peru.

H. a. assimilis (Elliot, 1876) - S Peru and NW Bolivia.

Descriptive notes. 9-10 cm; 5.0-6.0 g. Sexes alike. Bill blackish and straight. Entire plumage dark green, leg puffs in both sexes pale creamy buff to whitish; tail slightly forked, blue-black. Immature similar to adult but with brown fringes on head and neck feathers. Race *affinis* darker overall, with bluer tail and pale rufous leg puffs.

Habitat. Undergrowth of humid and wet pre-montane forest and forest borders from 1500 m to 3000 m altitude, rarely above 2500 m.

Food and Feeding. Territorial. Usually low at small groups of flowers; feeding territories are usually centred on a few flowering bushes. In-



sects are gleaned from leaves, hawking being less typical.

Breeding. Clutch size 2; incubation by female. No information on nest construction or breeding season available, but probably as in *H. aureliae*.

Movements. Probably disperses seasonally to lower temperate zone.

Status and Conservation. Not globally threatened. CITES II. Appears to be generally fairly common, though no precise data available. Race *affinis* known only from a few localities in Peru, notably Chirimoto, Utcubamba and Sira Pico.

Bibliography. Fjeldså & Krabbe (1990), Meyer de Schauensee (1982), Parker *et al.* (1982), Remsen & Traylor (1989), Stotz *et al.* (1996), Zimmer (1951b).

251. Hoary Puffleg

Haplophaedia lugens

French: Ériane givrée

German: Schuppenbauch-Hörschenkolibri

Spanish: Calzadito Canoso

Taxonomy. *Eriopus lugens* Gould, 1851, Quito, Ecuador.

Genus sometimes merged into *Eriocnemis*; also considered to be close to *Urosticte* and *Ocreatus*. Monotypic.

Distribution. Pacific slope of SW Colombia (Nariño) and NW Ecuador.



Descriptive notes. 9-10 cm; 5.0-6.0 g. Bill black and straight. Male bronze-green above becoming somewhat coppery on crown and especially on rump; underparts dark grey, the feathers edged white on throat and breast, flanks with greenish sheen; tail blackish and only slightly forked; leg puffs white, chestnut on inside. Female resembles male, but slightly duller, wings slightly shorter, leg puffs all white. Immature like female.

Habitat. Very wet pre-montane forest (cloud-forest), forest borders in foothills and lower highlands, and also in scrub. Typically found in low, dense vegetation at small clearings or

along ridges in primary forest, frequently in the vicinity of small streams; in secondary growth mainly low in bushes and shrubs. Occurs in upper tropical and subtropical zones. The species has been recorded at 1200-2000 m, regionally to 2500 m in Colombia; Ecuadorian records range from 1525 m to 2100 m; usually found at lower altitudes than *H. aureliae*.

Food and Feeding. Territorial; usually seen singly in dense understorey where feeds on nectar at small groups of flowers near ground and on bushes; rarely in canopy; prefers food plants with short corollas, for example *Palicourea*, *Besleria* and *Marantaceae*; takes insects by gleaning from leaves. In general, feeding habits are similar to those of *H. aureliae*.

Breeding. Breeding recorded in Aug. Nest is built mainly of moss and other plant material held together with spider webs forming a more or less ball-shaped structure; to protect it from rain and predation it is usually attached to the underside of a fern or large leaf at heights of 0.5-2 m. Clutch size 2; incubation 15-17 days, by female; chick flesh-coloured with two rows of grey-buff dorsal down; fledging period 20-24 days.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Currently considered Near-threatened. Restricted-range species: present in Chocó EBA. Confined to a rather small range in SW Colombia and NW Ecuador. Can still be found locally in Colombia (Pasto-Tumaco road, Ricaurte, San Pablo) and Ecuador (Carchi, Imbabura, Pichincha), but suitable habitat is rapidly disappearing due to extensive deforestation. The species depends on the conservation of appropriate habitats. Throughout its range species is protected in several reserves, for instance La Planada Reserve, Awá Indigenous Forest Reserve, Colombia (both rather small), and Cotacachi-Cayapas Ecological Reserve and Centro Científico Las Palmas in Ecuador.

Bibliography. Best *et al.* (1997), Butler (1979), Collar & Andrew (1988), Collar *et al.* (1992), Evans (1988), Fjeldså & Krabbe (1990), Hilty & Brown (1986), Kirwan & Marlow (1996), Meyer de Schauensee (1949), Orejuela (1987), Orejuela *et al.* (1982), Paynter & Traylor (1977, 1981), Renjifo *et al.* (1997), Salaman & Mazariegos (1998b), Schuchmann (1990a), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Wege & Long (1995).

Genus *UROSTICTE* Gould, 1853

252. Purple-bibbed Whitetip

Urosticte benjamini

French: Colibri de Benjamin

Spanish: Colibrí Puntablanca Occidental

German: Purpurbrustkolibri

Other common names: (Green-vented) Whitetip

Taxonomy. *Trochilus Benjamini* Bourcier, 1851, Gualea, Ecuador.

On the basis of behaviour, genus belongs to a clade including *Eriocnemis*, *Haplophaedia* and *Ocreatus*. Genus sometimes merged into *Adelomyia*. Sometimes considered conspecific with *U. ruficrissa*, based on intermediate characters of birds from NE Peru; this population has often been awarded race *intermedia*, but differences probably constitute a cline within present species; Peruvian population sometimes transferred to *U. ruficrissa*; more study required. Proposed race "rostrata" (W Colombia) is probably based on an aberrant individual. Monotypic.

Distribution. Pacific slope of W Colombia (headwaters of R San Juan) S to SW Ecuador (El Oro) and NE Peru.

Descriptive notes. 8-9 cm; 3.8-4.2 g. Male has medium-sized straight bill, black; above glittering green; prominent white postocular streak; underparts shining green with violaceous tinge below the throat, upper breast whitish, becoming greyish on belly, heavily spotted green; tail dusky bronze, central rectrices broadly tipped white, forming an oval spot. Female above similar to male, postocular stripe white; below white and heavily spotted with green; tail dusky bronze, purple subterminally,



outer rectrices broadly tipped white. Immature similar to adult female but with brown-edged head feathers.

Habitat. Forest and forest borders of montane regions at 700-1600 m. A solitary bird, foraging mainly inside the forest from near the ground to subcanopy level. In W Ecuador most numerous around 1200-1400 m.

Food and Feeding. Nectar of flowering Ericaceae, Rubiaceae and bromeliads. Insects are gleaned from the surface or caught in the air by hawking.

Breeding. Jan-Apr in Ecuador. Compact cup-shaped nest of moss and fern hairs is built in shrubs or vines along steep ravines, about 2-4 m above the ground. Clutch size 2; incubation 16-18 days, by female; chick is blackish with buffy dorsal down; fledging period unknown.

Movements. Sedentary in Colombia. In W Ecuador, after breeding, individuals disperse to lower altitudes.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Chocó EBA. A common bird in montane forests. Part of the range of the species is legally protected; occurs in Río Nambi Reserve (Colombia) and Cotacachi-Cayapas Ecological Reserve (Ecuador).

Bibliography. Best *et al.* (1997), Butler (1979), Davis (1986), Gerwin & Zink (1989), Hilty (1997), Hilty & Brown (1986), Kirwan & Marlow (1996), Meyer de Schauensee (1982), Parker *et al.* (1982), Salaman & Mazariegos (1998b), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Zimmer (1951a).

253. Rufous-vented Whitetip *Urosticte ruficrissa*

French: Colibri à sous-caudales rousses

Spanish: Colibrí Puntablanca Oriental

German: Rotsteißkolibri

Taxonomy. *Urosticte ruficrissa* Lawrence, 1864, Ecuador.

On the basis of behaviour, genus belongs to a clade including *Eriocnemis*, *Haplophaedia* and *Ocreatus*. Genus sometimes merged into *Adelomyia*. Sometimes considered conspecific with *U. benjamini*, based on intermediate characters of birds from NE Peru; this population has often been awarded race *intermedia*, but differences probably constitute a cline within *U. benjamini*; Peruvian population of *U. benjamini* sometimes transferred to present species; more study required. Monotypic.

Distribution. E slope of SC Andes of Colombia (Huila, SE Nariño) to E Ecuador.



Descriptive notes. 9-10 cm; 4-4.2 g. Male has medium-sized straight bill, black; upperparts shining green; white postocular streak; underparts shining green, undertail-coverts buffy; tail dusky bronze, deeply forked, central rectrices broadly tipped white. Female shining green above; white below with green spots, glittering on throat; tail dusky bronze, forked, outermost feathers broadly tipped white. Immature similar to adult female but with brown-edged head feathers.

Habitat. Humid, partly open mountain forest (including cloudforest) and forest edges from 1600 m to 2400 m. Forages from low to

middle strata.

Food and Feeding. Nectar of flowering *Clusia*, *Palicourea* and bromeliads. Insects are caught in the air by hawking, occasionally by gleaning from leaves.

Breeding. Jan-Apr. Compact cup-shaped nest is built of moss in vines, 2-4 m above the ground. Clutch size 2; incubation 15-18 days, by female; chick is blackish with sparse buffy dorsal down; fledging period 22-24 days (data from captive birds). First breeding in second year.

Movements. Sedentary, with local movements to higher altitudes after the reproductive period.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Colombian Inter-Andean Slopes EBA and Ecuador-Peru East Andes EBA. Generally uncommon throughout its range. Protected by national parks and nature reserves in most of its Colombian habitats; situation in Ecuador is more precarious due to heavy logging activities in areas of cloudforest.

Bibliography. Best *et al.* (1997), Fitzpatrick & Willard (1982), Gerwin & Zink (1989), Hilty & Brown (1986), Krüger *et al.* (1982), Renjifo *et al.* (1997), Ridgely & Gaulin (1980), Salaman & Mazariegos (1998a, 1998b), Schuchmann & Prinzing (1987), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Williams & Tobias (1994), Zimmer (1951a).

Genus *OCREATUS* Gould, 1846

254. Booted Racquet-tail *Ocreatus underwoodii*

French: Haut-de-chausses à palettes

Spanish: Colibrí de Raquetas

German: Grünscheitel-Flaggensylphe

Other common names: Racquet-tail, Racquet-tailed Hummingbird

Taxonomy. *Ornismya underwoodii* Lesson, 1832, Brazil; error = Santa Fé de Bogotá, Colombia. Based on display patterns, genus is closely related to *Urosticte*, *Eriocnemis* and *Haplophaedia*. Rufous-booted races *addae*, *annae* and *peruanus* sometimes considered to constitute one to three separate species. Proposed race *ambiguus* is synonymous with *incommodus*. Eight subspecies currently recognized.

Subspecies and Distribution.

O. u. polystictus Todd, 1942 - coastal mountains of N Venezuela (Carabobo to Miranda).

O. u. discifer (Heine, 1863) - NW Venezuela (Zulia and Falcón to Táchira and W Barinas) and NE Colombia (Norte de Santander).

O. u. underwoodii (Lesson, 1832) - E Andes of Colombia.

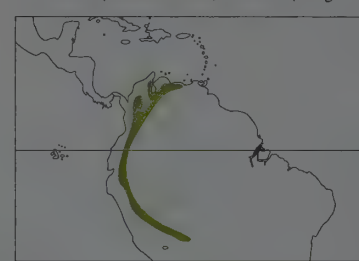
O. u. incommodus (Kleinschmidt, 1943) - W & C Andes of Colombia.

O. u. melanatherus (Jardine, 1851) - both slopes of Andes of Ecuador.

O. u. peruanus (Gould, 1849) - E Ecuador and NE Peru.

O. u. annae (Berlepsch & Stolzmann, 1894) - C & S Peru.

O. u. addae (Bourcier, 1846) - Bolivia (Yungas of La Paz to Santa Cruz and Chuquisaca).



Descriptive notes. Male 11-15 cm, (including elongated tail feathers), female 7-9 cm; 2.6-3.2 g. Male has short, straight, black bill; forehead bronzy, rest of upperparts and underparts mostly shining green; postocular spot white, throat and breast glittering green; leg puffs white or brown; tail deeply forked, outer rectrices elongated, ending in bare shafts and blue-black racquets. Female green above, postocular spot white, underparts white with green discs or green spots on sides only, small leg puffs white or buff; tail of ordinary length, forked, central feathers green, outer ones dark blue, tipped white. Immature similar to adult

female, but head feathers edged buff. Race *polystictus* similar to nominate, adult male more bronzy above, female more heavily spotted below; *discifer* similar to nominate but male usually has smaller and more rounded racquets; male of *incommodus* has smaller racquets than nominate, broad black chin and throat, female below almost pure white; *melanatherus* similar to previous race but with shorter bill and less extensive black on throat and under eye; *peruanus* differs from nominate by rufous leg puffs, bronzy tinge on forehead lacking, female darker green and more heavily spotted; *annae* differs from nominate by rufous leg puffs, tail shorter than in previous race, with streamers crossing; *addae* differs from nominate by rufous leg puffs, underparts whitish with dense green spotting, undertail-coverts green broadly-edged rufous, tail shorter with streamers crossing.

Habitat. Wet forest zone of subtropical and temperate Andean regions. Within forest as well as in open secondary growth from 1100 m to 3000 m, sometimes as low as 600 m, occasionally found at 4000 m, but most numerous at 1600-2200 m. Forages at low to high strata, 6-18 m.

Food and Feeding. Nectar of flowering *Palicourea*, *Clusia*, *Inga*, *Cavendishia* and bromeliads. Insects are caught in the air by hawking. Often several individuals feed in close proximity.

Breeding. Probably throughout the year; Jan-Apr in SW Colombia. Tiny cup-shaped nest of buffy plant fibre and lichen is placed on horizontal twigs in trees at 6-8 m above ground. Clutch size 2; incubation 16-17 days, by female; chick dark with brownish dorsal down; fledging at 19-22 days. First breeding in second year.

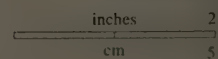
Movements. Seasonal altitudinal migration after breeding.

Status and Conservation. Not globally threatened. CITES II. A very common species in montane forest. Protected by several national parks and nature reserves throughout range, e.g. La Planada Reserve (Colombia). In S Colombia, above Cali and in Nariño, recorded densities of at least 2-3 pairs/km².

Bibliography. Best *et al.* (1997), Bleiweiss (1987), Bloch *et al.* (1991), Bond & Meyer de Schauensee (1943), Davies *et al.* (1994), Fjeldså & Krabbe (1990), Hilty (1997), Hilty & Brown (1986), Kleinschmidt (1949), Krüger *et al.* (1982), Merizalde de Albuja (1975), Meyer de Schauensee & Phelps (1978), Miller (1963), Mobbs (1975), Olrog (1963c), Parker *et al.* (1982), Ridgely & Gaulin (1980), Robens & Robens (1988), Rutgers & Norris (1972), Salaman & Mazariegos (1998a, 1998b), Schuchmann (1979c, 1987b), Schuchmann & Jakob (1981b), Schuchmann & Schuchmann-Wegert (1986), Snow & Snow (1980), Stotz *et al.* (1996), Williams & Tobias (1994), Zimmer (1930, 1951b).



PLATE 69



Genus *LESBIA* Lesson, 1832

255. Black-tailed Trainbearer

Lesbia victoriae

French: Porte-traine lesbie **German:** Schwarzschwanzsylphe **Spanish:** Colibrí Colilargo Mayor
Other common names: Long-tailed Trainbearer

Taxonomy. *Trochilus victoriae* Bourcier and Mulsant, 1846, Colombia. Differences in display and behaviour do not suggest particularly close relationship with *L. nuna*; may be more closely related to *Sappho sparganura*. Race *eucharis* of *L. nuna*, formerly thought to have come from Colombia, was provisionally placed in present species. Proposed race *aequatorialis* doubtfully distinct from nominate, since only difference documented is tail length which is quite a variable character within nominate. "*L. ortoni*" (= "*Zodalia glyceria*") is probably a hybrid of present species and *Ramphomicron microrhynchum*. Three subspecies recognized.

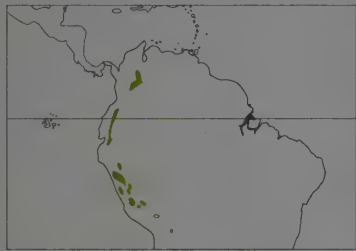
Subspecies and Distribution.

L. v. victoriae (Bourcier & Mulsant, 1846) - Andes of NE Colombia (Norte de Santander to Bogotá); Andes of S Colombia (Nariño) and Ecuador.

L. v. juliae (Hartert, 1899) - Andes of N & C Peru.

L. v. berlepschi (Hellmayr, 1915) - Andes of SE Peru.

Descriptive notes. 14.9-26 cm (including tail of 11.2-18 cm); c. 5-1 g. Male has slightly decurved bill, black; above shining bronzy-green, postocular spot white; iridescent emerald green gorget; rest of underparts tawny with green discs; small leg puffs; tail deeply forked, rectrices black with bronzy-green tips. Female similar to male, underparts buffy white with green discs, no gorget; tail shorter, deeply forked, rectrices shining bluish-black. Immature resembles adult female, immature male with partly developed gorget and streamers. Male of race *juliae* has shorter bill and tail, generally shining golden green; *berlepschi* has



bill more decurved, gorget iridescent grass green, lower underparts and undertail-coverts rusty.

Habitat. Forest edges on mountain slopes, *Polylepis* woodland, gardens and sub-*páramo* to *páramo* with scattered bushes, at 2600-4000 m.

Food and Feeding. Forages for nectar at middle to high strata of flowering Bignoniaceae, Fabaceae, Gesneriaceae, Leguminosaceae, *Puya* and introduced *Eucalyptus* trees. Insects are caught in the air by hawking.

Breeding. Oct-Mar (Quito), Sept-Oct (Bogotá), Jun-Aug (Nariño). Nest cup-shaped, interior made out of fine plant fibres, outside consists of moss and lichens; placed underneath rock or fern, suspended from twig, and also in bush. Incubation 18-19 days, by female; chick flesh-coloured with two rows of light brown dorsal down; fledging at 29-31 days. Nestling development prolonged.

Movements. Some altitudinal dispersal most likely following flowering season.

Status and Conservation. Not globally threatened. CITES II. Generally rather common. Although parts of habitat are heavily altered by human activities, including deforestation of *Polylepis* woodland and cattle-raising in sub-*páramo* and *páramo*, the species seems not to be affected. Readily accepts man-made habitats and is common in flowering gardens of Bogotá and Quito suburbs. In Ecuador, occurs in several protected areas such as Paschoa Forest Reserve and Cotopaxi National Park.

Bibliography. Berlioz (1932d), Best *et al.* (1997), Bloch *et al.* (1991), Butler (1979), Fjeldsá & Krabbe (1990), Fritsch & Schuchmann (1988), Graves (1997a), Hilty & Brown (1986), Kiff *et al.* (1989), King (1991), Moore (1947a), Morrison (1939), Parker *et al.* (1982), Rutgers & Norris (1972), Siegfried (1986), Snow (1983), Stotz *et al.* (1996), Zimmer (1930, 1951b).

256. Green-tailed Trainbearer

Lesbia nuna

French: Porte-traine nuna **German:** Grünschwanzsylphe **Spanish:** Colibrí Colilargo Menor

Taxonomy. *Ornismya nuna* Lesson, 1832, Peru.

Differences in display and behaviour do not suggest particularly close relationship with *L. victoriae*; probably closely related to *Ramphomicron*. Race *eucharis*, formerly thought to have come from Colombia, was provisionally placed in *L. victoriae*. Subspecific differences rather weak; proposed race *chlorigera* is synonym of *eucharis*; *boliviana* is synonym of nominate. Five subspecies currently recognized.

Subspecies and Distribution.

L. n. gouldii (Lodigies, 1832) - Andes of NE & SC Colombia; old record from Venezuela (Mérida).

L. n. gracilis (Gould, 1846) - Andes of Ecuador.

L. n. pallidiventris (Simon, 1902) - Andes of N Peru.

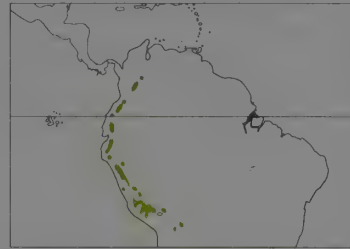
L. n. eucharis (Bourcier & Mulsant, 1848) - mountains near Huánuco (C Peru).

L. n. nuna (Lesson, 1832) - Andes of SW Peru and N Bolivia.

Descriptive notes. Male 15.3-17 cm (including tail of c. 10.6-12 cm), female c. 11-6 cm (including tail of c. 5-4 cm); c. 3-8 g. Male has very short, straight bill, black; entire plumage glittering emerald green, throat iridescent green, lower belly greyish with green discs; tail long, forked, black with green tips. Female similar to male, underparts white with glittering green discs; tail shorter. Immature similar to adult female, immature male with large green discs on throat. Male of *gouldii* similar to nominate, differing in smaller size, shorter bill and more green on tail; *gracilis* is similar but smaller with shorter, thicker bill, undertail-coverts buffish with green discs; *pallidiventris* has longer bill than previous two races, lighter and less blue-green upperparts; *eucharis* differs in pale coloration on outer webs of outermost rectrices.

Habitat. Second growth, bushy slopes, sometimes in *Polylepis* woodlands and *páramo* at 1700-3800 m.

Food and Feeding. Forages for nectar of flowering *Castilleja fissifolia*, *Cavendishia cordifolia*, *Rubus*, *Cuphea dipetala* and *Palicourea angustifolia*. Female defends small feeding territories. Forages at



low to medium heights. Insects are caught in the air by hawking during extended flights. Often recorded visiting *Espeletia* flowers to take out small insects such as *Tysanoptera*.

Breeding. Nov-Apr. Cup-shaped nest is built of moss and rootlets, lined with soft plant material; placed underneath overhangs on slopes 2-4 m above ground. Clutch size 2. No further information.

Movements. Some seasonal altitudinal movements most likely following breeding and flowering season.

Status and Conservation. Not globally threatened. CITES II. Locally fairly common. No im-

mediate threats identified; however, parts of habitat are endangered by deforestation of *Polylepis* woodlands, cattle-raising and agriculture. Occurs in Las Cajas National Recreation Area (Ecuador). Importation for wild-bird trade during recent decades has now ceased as a result of national and international regulations.

Bibliography. Berlioz (1932d), Best & Clarke (1991), Best *et al.* (1997), Bloch *et al.* (1991), Butler (1979), Cabot & Serrano (1988), Davies *et al.* (1994), Fjeldsá & Krabbe (1990), Hilty & Brown (1986), Koepcke (1970), Kraemer & Schmitt (1991), Meyer de Schauensee & Phelps (1978), Parker *et al.* (1982), Remsen & Traylor (1989), Rutgers & Norris (1972), Schuchmann (1983a, 1990a), Schmitt & Schmitt (1987), Schmitt *et al.* (1997), Snow & Snow (1980), Stotz *et al.* (1996), Taczanowski (1884), Williams & Tobias (1994), Wittmann (1982), Zimmer (1930, 1951b).

Genus *SAPPHO* Reichenbach, 1849

257. Red-tailed Comet

Sappho sparganura

French: Colibrí sappho **German:** Goldschwanzsylphe **Spanish:** Colibrí Cometa
Other common names: Comet Hummingbird, Fire-tailed/Sappho Comet

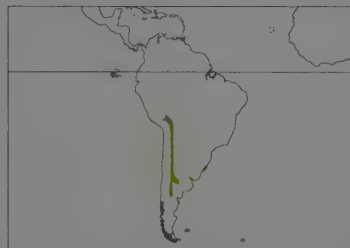
Taxonomy. *Trochilus sparganurus* Shaw, 1812, Peru; error = Bolivia.

Genus sometimes merged into *Lesbia*; may be closely related to *L. victoriae*. Two subspecies recognized.

Subspecies and Distribution.

S. s. sparganura (Shaw, 1812) - N & C Bolivia; possibly also extreme S Peru.

S. s. sappho (Lesson, 1829) - S Bolivia to N & W Argentina (Jujuy and Salta S to Neuquén) and marginally into CE Chile (Portillo Pass).



Descriptive notes. Male 19-20 cm (including tail of 7-10 cm), female 12-14 cm; 5-2.5-9 g. Male has short, slightly curved bill, black; head shining green, back rosy purple; throat glittering golden green, rest of underparts green; tail long, deeply forked, glittering golden purplish-rosy, each feather broadly tipped dusky purple. Female has upperparts shining green, rump purplish; throat buffy with green discs; underparts white, spotted green on sides; tail shorter and less deeply forked than in male, outermost rectrices with buffy white on outer web. Immature like adult female but head feathers fringed brown and with bronzy-green back.

Race *sappho* generally paler, with rosy purple replaced by golden orange.

Habitat. Arid to semi-arid open mountain slopes with scattered trees and bushy cover, semi-arid deciduous forest at 1500-4000 m; most numerous at 2000-2500 m during the breeding period, but occurs much lower during the southern winter at c. 1500 m. Forages mainly at low to medium heights.

Food and Feeding. Nectar of flowering *Dunalia*, *Acrnistus*, *Siphocampylus*, *Psittacanthus*, *Castilleja*, *Salvia*, *Nicotiana*, *Tripodanthus* and *Lamoureauxia*. Male establishes territories at nectar-rich food sources. Insects are caught in the air by hawking, sometimes gleaned from leaves.

Breeding. May-Jun in Bolivia, Oct-Dec in Argentina. Bulky cup-shaped nest of moss, lichen and animal hairs is built under rocks in steep ravines, often attached to rootlets; rarely nests in trees. Clutch size 2; incubation 19-20 days, by female; chick is darkish with brownish dorsal down; fledging at 31-32 days. First breeding in second year.

Movements. Mostly sedentary with seasonal altitudinal movements.

Status and Conservation. Not globally threatened. CITES II. A fairly common hummingbird; local densities of at least 3-4 pairs/km² in Santa Barbara Mts, Argentina. Protected in nature reserves and national parks throughout most of its range, such as El Rey and Calilegua National Parks (Argentina).

Bibliography. Babarskas *et al.* (1995), Bond & Meyer de Schauensee (1943), Butler (1926b), Canevari *et al.* (1991), Contino (1975), Fjeldsá & Krabbe (1990), Fjeldsá & Mayer (1996), Flores & Capriles (1998), Friedmann (1927), Galetto *et al.* (1993), González (1977), Johnson (1967), Montaldo (1995b), Narosky & Yzurieta (1993), Nellar (1993), Norez *et al.* (1983), de la Peña, M.R. (1994, 1997), Pereyra (1937, 1950), Remsen & Traylor (1989), Schuchmann (1982b), Serié & Smith (1923), Stotz *et al.* (1996), Todd (1942), Wetmore (1926), Zimmer (1952).

Genus *POLYONYMUS* Heine, 1863

258. Bronze-tailed Comet

Polyonymus caroli

French: Colibrí de Bourcier **German:** Rosenkehl sylphe **Spanish:** Colibrí Colibrone

Taxonomy. *Trochilus Caroli* Bourcier, 1847, no locality = Cajabamba, Peru. Genus sometimes merged into *Lesbia*; affinities uncertain, but probably closely related to *Taphrolesia*. Monotypic.

Distribution. C & S Peru; on Pacific slope; in W Andes (Cajamarca to W Arequipa); and from side valleys of R Marañón S to Huánuco and Huancavelica.



Descriptive notes. 11-13 cm; 5.1-5.6 g. Male has medium-sized, slightly decurved bill, black; above bronzy-green, postocular spot white; iridescent rosy purple gorget, rest of underparts bronzy-green, small white leg puffs; tail deeply forked, central rectrices bronze, outer ones purplish with bronze tips and white edges, underside steel blue. Female similar to male, gorget with shining orange discs, belly greyish with some green discs; tail less forked, shorter, central rectrices bronzy-green. Immature similar to adult female, immature male with some rosy discs on gorget, tail short, less forked, outer rectrices tipped white.

Habitat. Semi-arid mountain slopes with dense shrubs, cacti and *Agave* stands, edges of montane woodlands, at 1500-3600 m.

Food and Feeding. Little information; takes nectar of flowering *Agave*, *Phrygilanthus* and cacti; subordinate to other hummingbirds.

Breeding. Possibly Nov-Dec. No further information available.

Movements. Wide altitudinal range suggests some seasonal dispersal to lower or higher zones.

Status and Conservation. Not globally threatened. CITES II. Currently considered Near-threatened. Species appears to be locally common, but not well known; research required into biology and ecology.

Bibliography. Fjeldså & Krabbe (1990), Johnson (1967, 1972), Koeppke (1970), Meyer de Schauensee (1982), Olrog (1968), Parker *et al.* (1982), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Taczanowski (1884), Zimmer (1930, 1952).

Genus *RAMPHOMICRON* Bonaparte, 1850

259. Purple-backed Thornbill

Ramphomicron microrhynchum

French: Colibri à petit bec

German: Purpur-Kurzschnabelkolibri

Spanish: Colibrí Piquicorto Común

Taxonomy. *Ornismya microrhyncha* Boissonneau, 1840, Bogotá, Colombia.

Forms a superspecies with *R. dorsale*. Perhaps closely related to *Lesbia nuna*. Races *andicolum* and *albiventris* are doubtfully distinct from nominate. "*Lesbia ortonii*" (= "*Zodalia glyceria*") is probably a hybrid of present species and *L. victoriae*. Four subspecies recognized.

Subspecies and Distribution.

R. m. andicolum (Simon, 1921) - Andes of Venezuela (Mérida).

R. m. microrhynchum (Boissonneau, 1840) - Andes of Colombia, Ecuador and NW Peru.

R. m. albiventris Carriker, 1935 - Andes of C Peru (Huánuco to Cuzco and Apurímac).

R. m. bolivianum Schuchmann, 1984 - Andes of Bolivia (Cocapata in Cochabamba).



Descriptive notes. 8-9 cm; c. 3.5 g. Has shortest bill of any hummingbird, straight, black. Male upperparts metallic violet-purple, postocular spot white; gorget iridescent golden green, lower underparts bronzy-green, undertail-coverts coppery, fringed tawny; tail forked, dark purple. Female shining green above, postocular spot white; white below with large green discs, though belly lacks discs; tail less forked, dark bronzy-purple, outer pairs of rectrices tipped white. Immature resembles adult female, immature male with some purple on back. Race *andicolum* has gorget golden with green border, undertail-coverts more rufous;

albiventris has margins of undertail-coverts lighter, female has underparts with smaller discs; *bolivianum* is metallic violet above, underparts dark green, undertail-coverts greyish-white with black centres.

Habitat. Edges of humid montane forest, *Polylepis* forest, sub-*páramo* and *páramo* at 1700-3400 m. **Food and Feeding.** Feeds on nectar of flowering *Ericaceae*, *Lobeliaceae*, *Echeveria*, *Espeletia*, *Castilleja*, *Draba*, *Puya*, *Salvia* and *Geranium hirtum*. Insects are caught in the air byhawking and taken out of *Espeletia* flowers. Feeds trap-lining from medium heights to canopy. Often uses holes at base of corollas made by flowerpiercers (*Diglossa*).

Breeding. Possibly May-Sept (Colombia), one fledgling in Dec (Ecuador). Nest described as cup-shaped, made of fine plant fibres inside, moss decorated with lichens outside, placed on horizontal branch. Clutch size 2; incubation 16 days, by female.

Movements. Some altitudinal movements most likely.

Status and Conservation. Not globally threatened. CITES II. Generally uncommon throughout its extensive range. Natural habitat, *Polylepis* woodland and sub-*páramo*, in places under severe threat of deforestation; cattle-raising leads to overgrazing with a consequent loss of plant diversity. Regularly recorded in Puracé National Park (Colombia).

Bibliography. Berlioz (1932d, 1974), Best *et al.* (1997), Bloch *et al.* (1991), Butler (1979), Carriker (1935), Fjeldså (1995), Fjeldså & Krabbe (1990), Graves (1997a), Hilty & Brown (1986), Kraemer & Schmitt (1991), Meyer de Schauensee & Phelps (1978), Mobbs (1978), Moynihan (1979), Parker *et al.* (1982), Rasmussen *et al.* (1996), Remsen & Traylor (1989), Rüschi (1961e, 1973b, 1973d), Salaman & Mazariegos (1998b), Schuchmann (1984b, 1990a), Snow (1983), Snow & Snow (1980), Stotz *et al.* (1996), Taczanowski (1884), Zimmer (1952).

260. Black-backed Thornbill

Ramphomicron dorsale

French: Colibri à dos noir

German: Schwarzer Kurzschnabelkolibri

Spanish: Colibrí Piquicorto Dorsinegro

Taxonomy. *Ramphomicron dorsale* Salvin and Godman, 1880, Sierra Nevada de Santa Marta, Colombia.

Forms a superspecies with *R. microrhynchum*. Possibly closely related to *Lesbia nuna*. Monotypic.

Distribution. Santa Marta Mts of NE Colombia.



Descriptive notes. 9-10 cm; c. 3.5 g. Male has very short, slightly decurved black bill; upperparts velvety black, postocular spot white, uppertail-coverts purplish-bronzy on tips; olive green gorget, rest of underparts dark grey mixed with rufous, and with green discs; tail moderately long, deeply forked, purplish-black, outer pair of rectrices broadened. Female shining grass green above, uppertail-coverts as in male; buffy white below with some green discs; tail similar to male's but shorter, with outer pairs of rectrices tipped white. Immature unknown.

Habitat. Edges of humid and elfin forest, páramo from 2000 m to snow-line at 4600 m. Forages from low down to canopy.

Food and Feeding. Nectar of flowering *Ericaceae*, *Erythrina*, *Lobeliaceae*, *Melastomataceae*, *Puya*, *Rubiaceae* and *Salvia*. Often clings to flowers while feeding. Insects are caught in the air byhawking and gleaned from leaves.

Breeding. No information available.

Movements. Seasonal altitudinal movements to lower slopes in May-Jun.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Santa Marta Mountains EBA. Uncommon. Restricted range may render species vulnerable to habitat destruction. No immediate threats known; range protected by Sierra Nevada de Santa Marta National Park.

Bibliography. Fjeldså & Krabbe (1990), Hilty & Brown (1986), Meyer de Schauensee (1982), Olrog (1968), Mobbs (1978), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Todd & Carriker (1922).

Genus *OREONYMPHA* Gould, 1869

261. Bearded Mountaineer

Oreonympha nobilis

French: Colibri noble

German: Weißhalssylphe

Spanish: Colibrí Noble

Taxonomy. *Oreonympha nobilis* Gould, 1869, Tinta, 11,500 feet [c. 3500 m], Peru.

A distinctive species which may be closest to *Oxyptogon guerini*, based mainly on plumage coloration. Two subspecies recognized.

Subspecies and Distribution.

O. n. albolimbata Berlioz, 1938 - CW Peru (Huancavelica and S basin of R Apurímac).

O. n. nobilis Gould, 1869 - Andes of SC Peru (Apurímac and Urubamba Valleys, in Cuzco).



Descriptive notes. 14-17 cm (including tail of 6.5-8.5 cm); c. 9 g. Bill short, slightly decurved, black. Male has deep purplish-blue and black cap, and long, narrow emerald green to purplish "beard", often narrowly tipped blue; bronzy-black hood is demarcated by a whitish band slanting from nape to breast; body bronze-chestnut with white central underparts; deeply forked tail, outer rectrices with broad central white stripe down shaft. Female duller, and has smaller and more patchy "beard". Immature has duller hood with rather scaly pattern and whitish malar stripe. Race *albolimbata* has cap deep chestnut and black bordered with white.

Habitat. Bushy and lightly wooded places ranging from degraded land with *Nicotiana* bushes and *Eucalyptus* trees to mixed *Carica*, *Schinus* and *Tecoma* woodland with many columnar cacti, or mixed *Escallonia*/*Polylepis* woodlands with dense thorny scrub. Often near rocky outcrops or deep gorges, at 2500-3800 m.

Food and Feeding. Forages for nectar from flowers of *Agave*, columnar cacti, *Eucalyptus* and *Nicotiana*. Clings to the flowers or hovers below them with almost vertical body, incessantly spreading and closing tail. Also takes insects. Subordinate to other hummingbirds like *Patagona gigas* and *Colibri coruscans*.

Breeding. Nest undescribed; probably nests in caves and limestone gorges, perhaps especially in deep stream ravines.

Movements. Not known, although some seasonal shifts in habitat may be undertaken in response to variations in flowering.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Peruvian High Andes EBA. Fairly common locally, and can be found in quite degraded areas. However does not appear to be well established in any protected area.

Bibliography. Fjeldså (1992, 1995), Fjeldså & Kessler (1996), Fjeldså & Krabbe (1990), Meyer de Schauensee (1982), Morrison (1939, 1948), Olrog (1968), Parker & O'Neill (1980), Parker *et al.* (1982), Stotz *et al.* (1996), Taczanowski (1884), Zimmer (1953a).

Genus *OXYPOGON* Gould, 1848

262. Bearded Helmetcrest

Oxyptogon guerini

French: Colibri casqué

German: Helmkolibri

Spanish: Colibrí Chivito

Other common names: Guerini's Helmetcrest

Taxonomy. *Ornismia Guerinii* Boissonneau, 1840, Bogotá, Colombia. Closely related to *Oreonympha*, *Metallura* and *Chalcostigma*. Based on morphological differences, the races could be considered four separate species. Four subspecies recognized.
Subspecies and Distribution.
O. g. cyanolaemus Salvin & Godman 1880 - NE Colombia (Santa Marta).
O. g. lindenii (Parzudaki, 1845) - Andes of NW Venezuela (Mérida, Trujillo).
O. g. guerinii (Boissonneau, 1840) - E Andes of Colombia (S to Cundinamarca).
O. g. stuebelii A. B. Meyer, 1884 - C Colombia (Nevado del Ruiz).



Descriptive notes. 11.2-12.7 cm (including moderately long tail); male 4.9-6.2 g, female 4.4-5.2 g. Male has short, straight, black bill; head dark brown to black with white crest, back bronzy; white elongated chin and throat feathers form "beard" with green central feathers; white collar contrasts with dark head, rest of underparts greyish-bronzy; tail, forked, coppery to bronzy-green, has broad white stripe including shafts of outer rectrices. Female similar to male but lacks prominent crest and "beard", chin white with bronzy discs. Immature resembles adult female; immature male develops partial crest and "beard". Male of race *lindenii* has longer crest

than nominate, "beard" longest with only a few green discs, narrow white line on shafts of outer rectrices, female differs from nominate in having same tail coloration as male; in male *cyanolaemus* green of "beard" is replaced by purplish-blue, both sexes with extensive buff-white area on outer rectrices; male of *stuebelii* differs from other races in tan crest, "beard" tan on outer sides, centre proximally green becoming purple distally, outer rectrices with broad isabelline line in male and female.
Habitat. Humid open páramo with *Espeletia* vegetation, sometimes at edge of *Polylepis* forests; females often found in gorges while males seem to be more restricted to open hillsides; occurs at 3000 m to 5200 m.

Food and Feeding. Often seen at flowers of *Espeletia schultzei*, even on dry old ones which are full of insect larvae; other nectar sources are *Castilleja fissifolia*, *Draba lindenii*, *Echeveria venezuelensis* and *Siphocampylus planchonis*; clings to the flowers rather than hovering in front of them, using its tail for support like a woodpecker. Often sits on ground to pick up disturbed arthropods, mainly Diptera flies, Hymenoptera and spiders; catches them by hovering jumps, or hawks for them from a perch or ground, often flying low above running water.

Breeding. Season closely related to flowering season of *Espeletia*; usually Jun/Jul-Oct/Nov (Venezuela). Nest large, made out of fibres from *Espeletia*; found mainly at riverbanks in small cavities near waterfalls, underneath rocks or overhanging plants, or in clefts in rocks near running water, protected from sunlight and rain; sometimes same nest locality is used for several years, new nest often constructed on top of previous year's nest. Sometimes several nests are placed close to each other, so female territoriality is absent. Clutch size 2, eggs rather large compared to female's body size; laying interval 3-4 days; incubation 21-23 days, by female. Chick naked, light flesh-coloured with two rows of white dorsal down; very slow nestling development, fledging at 35-38 days; after fledging returns to nest for several more nights.

Movements. Present all year round in páramo, but part of population in Venezuela seems to migrate to lower elevations at edges of *Polylepis* woodland or more bushy páramo during dry season in Jan/Feb; few records of individuals below 2300 m at this time of year.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Cordillera de Mérida EBA, Santa Marta Mountains EBA, Colombian East Andes EBA and Central Andean Páramo EBA. Common locally. Races *cyanolaemus*, *stuebelii* and *lindenii* have highly restricted ranges. Race *lindenii* is the most abundant species within its habitat, which is protected in two national parks (Sierra Nevada and Sierra La Culata), where recorded local densities are of at least 4-5 pairs/km²; however, overgrazing of these habitats may affect the native flora, including food plants of this species.

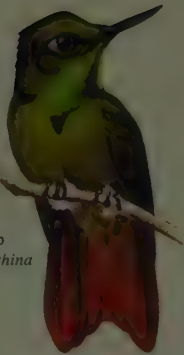
Bibliography. Berlioz (1964), Berry & Calvo (1989, 1994), Dorst & Vuilleumier (1986), Fjeldså & Krabbe (1990), Hilty (1994), Hilty & Brown (1986), Kleinschmidt (1935), Meyer de Schauensee & Phelps (1978), Peyre de Fabrègues (1990), Ruschi (1961f, 1973b, 1973d), Snow (1983), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Todd & Carraker (1922), Vélez & Velázquez (1998), Vuilleumier (1986), Vuilleumier & Ewert (1978), Wolf & Gill (1986), Züchner (1998).

PLATE 70

inches 2
cm 5



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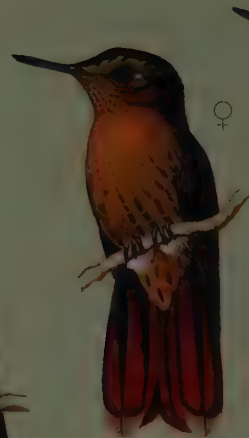
ssp
tyrianthina



ssp oreopola ♂



♂
ssp
malagae



♀



264



ssp districta ♂

263



ssp
smaragdincollis



265

ssp aeneocauda



ssp theresiae ♂

267



ssp parkeri ♂



♀

266



♂



♀



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268



♂



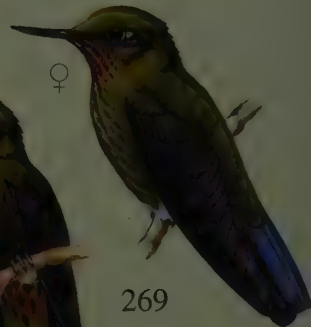
♂

ssp primolinus



♂

269



♀



ssp williamsi

♀

♂



270



♂

ssp
steinslandi



♂

ssp
recisa



271



♀

Genus *METALLURA* Gould, 1847

263. Tyrian Metaltail

Metallura tyrianthina

French: Métallure émeraude

Spanish: Metallura Tiria

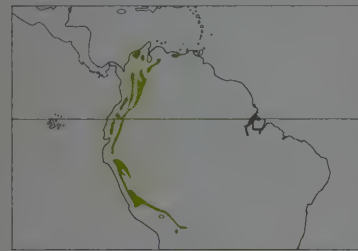
German: Smaragdkehl-Glanzschwänzchen

Taxonomy. *Trochilus tyrianthinus* Loddiges, 1832. Popayán, Colombia. Geographical variation is complex, reflecting a southern origin and progressive morphological change in respect of female throat and breast coloration towards north. Race *districta* in N Colombia forms "leapfrog" pattern with race *smaragdinicollis* in Peru and N Bolivia. Proposed race *peruviana* synonymous with *smaragdinicollis*. Seven subspecies recognized.

Subspecies and Distribution.

- M. t. districta* Bangs, 1899 - Santa Marta and Perijá Mts (NE Colombia).
- M. t. chloropogon* (Cabanis & Heine, 1860) - Caribbean coastal range (N Venezuela).
- M. t. oreopola* Todd, 1913 - Andes of Venezuela (Lara, Trujillo, Mérida).
- M. t. tyrianthina* (Loddiges, 1832) - NW Venezuela (SW Táchira) through all Andean chains of Colombia and E & S Ecuador to extreme N Peru.
- M. t. quitensis* Gould, 1861 - NW Ecuador.
- M. t. septentrionalis* Hartert, 1899 - Andes of Peru (W of R Marañón).
- M. t. smaragdinicollis* (d'Orbigny & Lafresnaye, 1838) - E Andes of Peru and N Bolivia.

Descriptive notes. 9-10 cm; 3.4-3.6 g. Male has short, straight, black bill; upperparts bottle green, underparts green with whitish-grey feather fringes; throat patch emerald green; slightly forked tail glistening bronze. Female has underparts whitish with green spots; chin, throat and upper breast ochre-orange covered with olive green dots; outer tail feathers with whitish tips. Immature similar to adult female. Race *districta* has violet tail, spots on throat and upper breast of female completely lacking; *chloropogon* has coppery red tail, male almost completely black, female almost without spots on throat and upper breast; *oreopola*



has golden red tail, male has feathers of upperparts with coppery subterminal bars, underparts green with grey fringing, female almost without spots on throat and upper breast; *quitensis* resembles nominate, but has longer bill and bronze-olive tail; *septentrionalis* has purple-blue tail shot with green, male underparts white with bronze olive spots; *smaragdinicollis* similar to *districta* but female heavily spotted on throat and upper breast.

Habitat. Occurs in the interior of rather open humid forest, including second growth, cloudforest and moss-clad tree-line scrub; in small patches of *Tilandsia*-clad wood in semi-arid valleys or in elfin forest patches. Occasionally in areas of ecotone between stunted woodland and páramo, or at patches of brush in lower páramo. Locally displaced from tree-line habitats to lower altitudes by members of the *Metallura aeneocauda* superspecies in those places where this zone is in a fairly pristine state. Ranges altitudinally between 1500 m and 4200 m, most common at 2500-3300 m; in the coastal mountains of Venezuela most numerous around 2000 m. Forages at the outer canopy of bushes and medium-sized trees.

Food and Feeding. Recorded at open flowers of *Berberis*, *Escallonia*, *Eucalyptus*, *Eugenia*, *Hesperomelas*, *Gaultheria rufescens*, *Palicourea angustifolia*, *Palicourea anacardifolia*, *Manettia coccocypseloides*, *Rubus*, some melastomes, solenads, ericads and *Salvia*. Forages in hover-flight or clings to flowers while feeding on nectar. Occasionally pierces bases of flowers with long corollas. Insects are caught in the air by hawking. Male establishes feeding territories.

Breeding. Birds in breeding condition Apr-Aug in Perijá Mountains and in E and C Andes of Colombia. Specimens with enlarged gonads found Oct in Ecuador, Jun-Aug in N Bolivia. Eggs in Oct-May (Jun) in W Ecuador. Nest-building female in Jul at Cerro Fonté, E Andes of Colombia. Nest in a pendent mass of moss in a rocky niche or among roots of overhanging bank, 1.8-3 m above the ground. Nest in Cerro Fonté made of moss with pieces of fern and plant fibre with small nest chamber partially roofed over with moss, lacking lining material. Clutch size 2; incubation by female. First breeding in second year.

Movements. Seasonal altitudinal movements; casually down to 600 m in Venezuela.

Status and Conservation. Not globally threatened. CITES II. Common throughout its extensive range, locally very abundant. Presently not at risk due to its wide distribution and its relatively generalized habitat requirements; less sensitive to man-induced environmental changes than other *Metallura* species and appears to be favoured by moderate forest disturbance. Occurs in Las Cajas National Recreation Area (Ecuador).

Bibliography. Baez *et al.* (1997), Best *et al.* (1997), Bloch *et al.* (1991), Bond & Meyer de Schauensee (1943), Boucard (1893), Butler (1979), Carraker (1935), Davies *et al.* (1994), Fjeldså & Krabbe (1990), García-Moreno *et al.* (1999), Heindl & Schuchmann (1998), Hilty & Brown (1986), Koepeke (1954, 1958, 1961, 1970), Meyer de Schauensee & Phelps (1978), Moore (1934b, 1947a), Niethammer (1953), O'Neill & Parker (1978), Parker, Parker & Plenge (1982), Parker, Schulenberg *et al.* (1985), Remsen (1984, 1985), Remsen, Traylor & Parkes (1986), Salaman & Mazariegos (1998a, 1998b), Snow, B. K. (1980), Snow, D. W. & Snow (1980), Stotz *et al.* (1996), Vigors (1832), Williams & Tobias (1994), Zimmer (1930, 1952).

264. Perijá Metaltail

Metallura iracunda

French: Métallure dorée

German: Rotschwanz-Glanzschwänzchen

Spanish: Metallura Iracunda

Taxonomy. *Metallura iracunda* Wetmore, 1946, above Airoca, Sierra de Perijá, Magdalena, Colombia.

Most closely related to *M. tyrianthina*, but sympatric with it. Monotypic.

Distribution. Perijá Mts of N Colombia and adjacent Venezuela (Cerro Pintado, Cerro Tetari and probably Sabana Rubia).



Descriptive notes. 10-11 cm; 3.6-4.1 g. Larger and darker than sympatric *M. tyrianthina districta*, but in coloration similar to smaller *M. t. chloropogon*. Male has short, straight, black bill; upperparts almost black with golden reflections, below very dark bronzy-green with golden sheen; glittering emerald green throat patch; slightly forked tail glittering ruby red. Female has rich buff underparts with bronzy-green spots; chin, throat and upper breast ochre-orange, sparsely covered with olive green spots; outer tail feathers tipped buffish. Immature similar to female.

Habitat. Recorded from rather open bushy terrain near summits and forest borders between 2800 m and 3200 m. Cerro Pintado is a unique karstic environment covered by elfin forest, *Swallenochloa* bamboo and grass páramo, and isolated by vertical cliffs. Cerro Tetari is a sandstone area with somewhat different vegetation. Forages in low to medium, sometimes upper strata.

Food and Feeding. No information.

Breeding. No information.

Movements. No information, but presumably sedentary.

Status and Conservation. Not globally threatened. CITES II. Currently considered Near-threatened. Restricted-range species; present in Colombian East Andes EBA. The species may be vulnerable owing to its very small range; studies of its ecology and its sensitivity to man-induced environmental changes are therefore badly needed. Its range is situated in a border mountain range with much illegal activity such as smuggling, drug cultivation and dealing, uncontrolled colonization and obscure interests in mineral exploitation. There are many roads approaching the mountains on the Colombian side, and because of problems of logistics it is difficult to implement the protection of the Venezuelan Perijá National Park. Fortunately, Cerro Tetari remains essentially pristine. Cerro Pintado is N of the protected area, but because access is difficult human activities there seem to be very limited. Inhabitants of the village of Villanueva, on the Colombian side, are trying to protect the natural habitat of the Cerro Pintado area.

Bibliography. Fjeldså & Krabbe (1990), García-Moreno *et al.* (1999), Heindl & Schuchmann (1998), Hilty & Brown (1986), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Olrog (1968), Renjifo *et al.* (1997), Stattersfield *et al.* (1998), Stotz *et al.* (1996).

265. Scaled Metaltail

Metallura aeneocauda

French: Métallure à queue d'airain

Spanish: Metallura Escamosa

German: Schuppenbauch-Glanzschwänzchen

Other common names: Andean Metaltail; Brassy Metaltail (*aeneocauda*); Reddish Metaltail (*malagae*)

Taxonomy. *Trochilus* (—?) *aeneocauda* Gould, 1846, Bolivia.

Forms superspecies with *M. eupogon*, *M. theresiae*, *M. odomae*, *M. baroni* and *M. williamsi*. Race *malagae* formerly considered to be distinct species, but in context of typical infraspecific variation within present genus morphological differences justify only subspecific separation. Two subspecies recognized.

Subspecies and Distribution.

- M. a. aeneocauda* (Gould, 1846) - E Andean slopes from SE Peru (Cordillera Vilcabamba) to NW Bolivia (Yungas of La Paz).
- M. a. malagae* Berlepsch, 1897 - Incachaca in Yungas of Cochabamba (C Bolivia).



Descriptive notes. 12-13 cm; 5.2-5.4 g. Male has medium-sized, straight, black bill; upperparts bottle green, underparts appear scaly due to tan feather margins; throat patch iridescent bright green; slightly forked tail iridescent sky blue and bronzy-green above, glittering green below. Female similar but more mottled below, with only feather centres green; throat patch incomplete; outer tail feathers with pale tips. Immature similar to female. Race *malagae* has longer bill; tail bronzy-red above and red below.

Habitat. Bushy glades in cloudforest and at tree-line, and sometimes on humid rocky slopes with herbs, low shrubs and occasional bushes. Ranges between 2500 m and 3600 m, but mostly well above 3000 m. Forages hovering within 2 m of the ground.

Food and Feeding. Nectar of *Berberis*, *Brachyotum*, *Centropogon*, *Gentiana*, *Ribes* and other flowers with 2-4 cm corollas, to which they often cling. Feeds extensively on insects. Male establishes feeding territories.

Breeding. Specimens with enlarged gonads found in May and Jun. Clutch size 2; incubation by female. No further information.

Movements. No information; but presumably sedentary. Individuals sometimes disperse high up into the páramo zone and possibly also down into the montane forest.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Bolivian and Peruvian Upper Yungas EBA. Fairly common locally. Species not at risk at present, due to its fairly wide distribution and its rather unspecialized ecology. In the context of its small range, may be vulnerable in places because regular grassland burning has destroyed the natural tree-line habitat over large areas. Protected within the upper Manu National Park in Peru and Carrasco-Ichilo National Park in Bolivia.

Bibliography. Bond & Meyer de Schauensee (1943), Fjeldså (1992, 1995), Fjeldså & Kessler (1996), Fjeldså & Krabbe (1990), García-Moreno *et al.* (1999), Graves (1980), Heindl & Schuchmann (1998), Hinojosa *et al.* (1998), Kessler & Herzog (1998), Niethammer (1953), Parker & O'Neill (1980), Parker *et al.* (1982), Remsen (1984, 1985), Remsen & Traylor (1989), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Zimmer (1952).

266. Fire-throated Metaltail

Metallura eupogon

French: Métallure à gorge feu

Spanish: Metalura Barbafeugo

German: Feuerkehl-Glanzschwänzchen

Taxonomy. *Urolampira eupogon* Cabanis, 1874, Maraynioc, Junín, Peru.Forms superspecies with *M. aeneocauda*, *M. theresiae*, *M. odomae*, *M. baroni* and *M. williami*. Sometimes considered to include *M. odomae* and (in past) *M. baroni* as races, but differences in coloration, together with geographical separation, justify their treatment as separate species. Monotypic.**Distribution.** E slope of Andes in C Peru, from immediately S of R Hualлага in Huánuco to R Apurímac.**Descriptive notes.** 11 cm; 5.0 g. Male has medium-sized, straight, black bill; upperparts and underparts almost uniformly yellowish olive-green covered with bronzy reflections; narrow throat patch orange; tail iridescent sky blue tinged with green above, glittering yellow-green below. Female similar to male but throat patch incomplete; outer tail feathers with pale tips. Immature similar to female.**Habitat.** Open glades with Melastomataceae and Ericaceae shrubs in humid moss-clad dwarf and elfin forest alternating with *pajonal* (Andean grass steppe), and shrubby habitats along the tree-line. Also straggles into adjacent *páramo* grassland. Ranges between 2900 m and 4000 m, commonest above 3500 m.**Food and Feeding.** No information. Probably as other members of the *M. aeneocauda* superspecies.**Breeding.** Specimens with enlarged gonads found in Jun and Jul. Clutch size 2; incubation by female. No further information.**Movements.** No information; but probably sedentary. May undertake seasonal altitudinal movements. **Status and Conservation.** Not globally threatened. CITES II. Restricted-range species: present in North-east Peruvian Cordilleras EBA. Locally fairly common. Presently not at risk due to its wide distribution and its generalized ecology. Occurs in the Yanachaga-Chemellén National Park, and probably also in the Pui-Pui Protection Forest. However, the species may be vulnerable because of its small range, where burning to sustain very extensive cattle-ranching is widely practised and has considerably altered the tree-line habitat.**Bibliography.** Fjeldså (1995), Fjeldså & Krabbe (1990), García-Moreno *et al.* (1999), Graves (1980), Heindl & Schuchmann (1998), Meyer de Schauensee (1982), Olog (1968), Parker *et al.* (1982), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Zimmer (1930, 1952).

267. Coppery Metaltail

Metallura theresiae

French: Métallure de Thérèse

German: Kupferglanzschwänzchen

Spanish: Metalura de Teresa

Taxonomy. *Metallura theresiae* Simon, 1902, Tayabamba, Department of Pataz, Peru.Forms superspecies with *M. aeneocauda*, *M. eupogon*, *M. odomae*, *M. baroni* and *M. williami*. Two subspecies recognized.**Subspecies and Distribution.***M. t. parkeri* Graves, 1981 - Cordillera de Colán (N Peru).*M. t. theresiae* Simon, 1902 - both slopes of Andes E of R Maraón and S to Cordillera Carpath N of R Hualлага, Huánuco (NE Peru).**Descriptive notes.** 11 cm; 4.8-5.0 g. Male has medium-sized, straight, black bill; upperparts and underparts olive-bronze with strong coppery red reflections, especially on head; throat patch narrow, bright shiny green; tail shining violet-blue above, glittering grey-violet below. Female similar to male, but throat patch duller and incomplete; outer tail feathers with whitish tips on underside. Immature similar to female. Race *parkeri* lacks coppery red reflections and has a green crown; tail sky blue above and yellowish-green below.**Habitat.** Occurs in open glades with Melastomataceae and Ericaceae shrubs in humid dwarf and elfin forest with mosses and lichens, and in scrub bordering boggy grassland; forages from understorey to canopy. Ranges between 2900 m and 3800 m.**Food and Feeding.** Mostly feeds in hover-flight from Melastomataceae flowers (*Brachyotum*, *Macleania*). Male establishes feeding territories.**Breeding.** Specimens with enlarged gonads found in Aug and Sept. Clutch size 2; incubation by female. First breeding in second year.**Movements.** No information; presumably sedentary but seasonal altitudinal movements might occur. **Status and Conservation.** Not globally threatened. CITES II. Restricted-range species: present in North-east Peruvian Cordilleras EBA. Locally common. The species is under pressure from habitat degradation due to grazing and burning of *páramo* grassland, and appears to be considerably more numerous in undisturbed tall-grass and shrubby *páramo* than in areas that have been burned and grazed for many years. Range includes the Río Abiseo National Park; however, protection in the Bosque Unchog area in Cordillera Carpath is also desirable.**Bibliography.** Fjeldså (1995), Fjeldså & Krabbe (1990), García-Moreno *et al.* (1999), Graves (1980, 1981), Heindl & Schuchmann (1998), Meyer de Schauensee (1982), Olog (1968), Parker, Parker & Plenge (1982), Parker, Schultenberger *et al.* (1985), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Zimmer (1952).

268. Neblina Metaltail

Metallura odomae

French: Métallure de Chinguela

Spanish: Metalura del Chinguela

German: Purpurkehl-Glanzschwänzchen

Taxonomy. *Metallura odomae* Graves, 1980, Cerro Chinguela, c. 5 km north-east of Sapalache, Piura, Peru.Forms superspecies with *M. aeneocauda*, *M. eupogon*, *M. theresiae*, *M. baroni* and *M. williami*; recently recorded as occurring sympatrically with *M. williami atrigularis* in Podocarpus National Park (S Ecuador), indicating that this part of superspecies may not hold good. Sometimes considered to be a race of *M. eupogon*, but differences in coloration, together with geographical separation, justify their treatment as separate species. Monotypic.**Distribution.** S Ecuador (S Loja) and adjacent extreme N Peru (N Piura).**Descriptive notes.** 10-11 cm; 4.8-5.2 g. Male has medium-sized, straight, black bill; upperparts yellowish olive-green, underparts yellowish olive-green with pale feather fringes; auriculars and lores with coppery reflections; throat patch dark red; tail sky blue tinged with green above, glittering yellow-green below, whitish tips on outer tail feathers. Female similar to male, but throat patch incomplete and scarlet. Immature similar to female.**Habitat.** *Pajonal* of humid tree-line type with forested ravines and patches of mossy elfin forest well above the tree-line, on windswept,foggy and rainy *páramo*; forages from understorey to canopy. Ranges between 2600 m and 3350 m. **Food and Feeding.** Recorded taking nectar from flowers of *Brachyotum*, from a *Berberis*-like shrub, and from white flowers of a dwarf ericaceous shrub. Insects are caught in the air by hawking. Male establishes feeding territories.**Breeding.** Presumed peak in season Nov-Feb. In late Aug 1989, one nest found on Cerro Chinguela at 2850 m consisted of a mossy cup covered with pale lichens and possibly held together with spider web, and was placed c. 2 m above ground in a small rock-ledge cavity sheltered from the prevailing wind. Clutch size 2; incubation by female.**Movements.** Remains in its exposed habitat even during very bad weather, when five other species of hummingbirds sharing this habitat forage in more sheltered ravines. However, casual observation in bushy parts of the upper montane forest suggests slight altitudinal dispersal.**Status and Conservation.** Not globally threatened. CITES II. Currently considered Near-threatened. Restricted-range species: present in Central Andean *Páramo* EBA. On Cerro Chinguela, reported to be fairly common, but at low densities; this assessment also applies to the population within Podocarpus National Park, but despite its reasonable abundance the species may be vulnerable owing to its restricted distribution. The inhospitable climate of the region it inhabits offers some protection against intrusion by man. However, the Cerro Chinguela *páramo* is grazed by small numbers of cattle, and is burned almost annually by local herders. Most of the Podocarpus National Park was open to gold mining until 1993; when the concession was lifted, following an international campaign, only a small part had been mined; casual gold prospectors and settlers, who had already established some dwellings and small-scale logging concerns inside the park, are now pushing for access, and pressure is likely to increase greatly in future. For the adequate protection of the species the future of Cerro Chinguela must be secured. The species also occurs in the Tabaconas-Namballe National Sanctuary in Peru.**Bibliography.** Best & Kessler (1995), Best *et al.* (1997), Bloch *et al.* (1991), Collar & Andrew (1988), Collar *et al.* (1992), Fjeldså (1992, 1993, 1995), Fjeldså & Krabbe (1990), García-Moreno *et al.* (1999), Graves (1980), Heindl & Schuchmann (1998), Hinkelmann (1987), Krabbe *et al.* (1997), Parker, Parker & Plenge (1982), Parker, Schultenberger *et al.* (1985), Rahbek *et al.* (1995), Rasmussen *et al.* (1996), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Taylor (1995), Vuilleumier & Mayr (1987), Wege & Long (1995), Williams & Tobias (1994).

269. Violet-throated Metaltail

Metallura baroni

French: Métallure de Baron

Spanish: Metalura de Azuay

German: Violettekehl-Glanzschwänzchen

Taxonomy. *Metallura baroni* Salvin, 1893, mountains near Cuenca, 12,000 feet [c. 3660 m], Ecuador. Forms superspecies with *M. aeneocauda*, *M. eupogon*, *M. theresiae*, *M. odomae* and *M. williami*; recently recorded as occurring sympatrically with *M. williami atrigularis* at R Mazan in Azuay (S Ecuador), though altitudinally segregated, occurring at higher elevations. Formerly considered conspecific with *M. eupogon*, but differences in coloration, in combination with isolated distribution, support separate species status. Monotypic.**Distribution.** SC Ecuador, on both slopes of Cajas Plateau W of Cuenca (Azuay).**Descriptive notes.** 10-11 cm; 4.2-4.5 g. Male has medium-sized, straight, black bill; upperparts and underparts uniformly dark olive green; throat patch purple-violet; tail iridescent violaceous sky blue above, glittering yellow-green below. Female has underparts whitish-grey, densely spotted with olive green; throat patch incomplete; outer tail feathers with whitish tips on underside. Immature similar to female.**Habitat.** Edges of moist elfin forest and *Polylepis* woods with boulders draped with bromeliads, ericads, orchids, ferns and mosses, and on areas of adjacent *páramo*. Between

3150 m and 3700 m; one reported sighting at 1900 m in low, shrubby, riparian growth in the arid Ona Valley. Forages from undergrowth to canopy.

Food and Feeding. Feeds in hover-flight taking nectar from *Duranta*, *Macleania* and other shrubby ericads, from the parasitic *Tristerix longibracteatus* (Lorantheaceae), and from *Castilleja fissifolia*. Male establishes feeding territories.**Breeding.** Probably nests Nov-Feb. At type locality a nest with one egg was found in Apr; nest had shape of a slipper without heel and was made of moss, twigs, wool and other similar materials. Clutch size 2; incubation by female.**Movements.** No information; presumably sedentary but seasonal altitudinal movements possible. If sighting in Ona Valley is reliable, it may reflect wandering behaviour.**Status and Conservation.** **VULNERABLE.** CITES II. Restricted-range species: present in Central Andean *Páramo* EBA. Total population is suggested by extrapolation to reach well over 2000 birds, but has presumably been declining with steady habitat destruction since 1970's. Population

may now be stabilizing, as conservation is implemented in the key area of Río Mazan, which supports a population of 50-100 individuals. Río Mazan, a small reserve at the edge of Cajas National Recreation Area, was saved from clear-felling in 1981; there, present species is reported to be the commonest hummingbird at 3400 m. For the conservation of this species, effective protection of Cajas National Recreation Area must be ensured, and páramo E & S of Cuenca should be surveyed for possible occurrence of the species.

Bibliography. Anon. (1984b), Barnett & Gretton (1987), Best *et al.* (1997), Butler (1979), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Fjeldså (1992, 1995), Fjeldså & Krabbe (1990), García-Moreno *et al.* (1999), Graves (1980), Gretton (1986), Hartert & Hartert (1894), Heindl & Schuchmann (1998), King (1988, 1989), Ortiz (1984), Ridgely (1980), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Taylor (1995), Wege & Long (1995), Williams & Tobias (1994), Zimmer (1952).

270. Viridian Metaltail

Metallura williami

French: Métallure verte **German:** Grünes Glanzschwänzchen **Spanish:** Metalura Verde
Other common names: Colombian Metaltail (*recisa*); Ecuadorian Metaltail (*primolinus*); Black-throated Metaltail (*atrigrularis*)

Taxonomy. *Trochilus williami* DeLattre and Bourcier, 1846, vicinity of Popayán, Colombia. Forms superspecies with *M. aeneocauda*, *M. eupogon*, *M. theresiae*, *M. odomae* and *M. baroni*; recently recorded as occurring sympatrically with *M. odomae* in Podocarpus National Park (S Ecuador), indicating that this part of superspecies may not hold good; also recently found to be sympatric with *M. baroni* at R Mazan in Azuay (S Ecuador), though altitudinally segregated, occurring at lower elevations. Some authors have considered the races to constitute four distinct species. Races *primolinus* and *atrigrularis* form a zone of intergradation in C Ecuador (Chimborazo). Race *primolinus* sometimes misspelt as *primolina*, but is masculine noun based on name of Prince Primoli, grandson of C. L. Bonaparte. Four subspecies currently recognized.

Subspecies and Distribution.

M. w. recisa Wetmore, 1970 - Páramo de Frontino in Antioquia (NC Colombia).
M. w. williami (DeLattre & Bourcier, 1846) - both slopes of C Andes in Colombia.
M. w. primolinus Bourcier, 1853 - E Andes of S Colombia (Nariño) and N Ecuador.
M. w. atrigrularis Salvin, 1893 - S Ecuador, in Azuay and Loja (Cordillera de Chilla).



Descriptive notes. 11-12 cm; 4.2-4.8 g. Male has medium-sized, straight, black bill; upperparts and underparts bottle green with broad glittering throat patch of same colour as body plumage, but more vivid; tail glittering purplish-blue above, silky purplish-blue below, slightly forked. Female mottled below, with only centres of feathers green; throat patch incomplete; outer tail feathers with whitish tips on underside. Immature similar to female. Race *recisa* differs by relatively short bill and more forked tail, shining green below; *primolinus* has tail reddish-black above and shining green below, only narrowly forked; *atrigrularis* has a

black blotch in the centre of throat patch, tail shining green below, only narrowly forked.

Habitat. In páramo grassland with scattered bushes, and in shrubby stunted borders of humid montane dwarf forest and elfin forest with mosses and lichens. Common between 2700 m and 3600 m in Ecuador, up to 4000 m in Colombia; occasionally down to 2100 m. Recorded at lower altitude than *M. baroni* at R Mazan (S Ecuador). Forages from undergrowth to canopy.

Food and Feeding. Feeds while hovering on nectar of mainly Ericaceae and Melastomataceae shrubs. Male establishes feeding territories.

Breeding. Individuals in breeding condition Feb and late Mar in C Andes of Colombia, and in Aug at N end of W Andes, Colombia; in Ecuador specimens with enlarged gonads found Mar and Jun, and active nests recorded Jul and Aug. On Mt Sangay, Ecuador, 6 nests, all within 1.5 km of each other, were found on roots or in rocky niches clad with mosses and lichens, sometimes sheltered under blades of *paja* grass, and placed above mountain torrents; made of moss without special outer layer; interior lined with cottony white plant down and small feathers. Clutch size 2; incubation by female. First breeding in second year.

Movements. No information, but presumably sedentary. Males may disperse to particularly high altitude outside the breeding season.

Status and Conservation. Not globally threatened, CITES II. Occurs in suitable habitats only in low numbers. Regular burning of the páramo slopes to support extensive cattle-grazing has destroyed the natural habitat in large parts of the range. Conservation status of race *recisa* unclear, but other taxa are variously protected in Los Nevados, Las Hermosas and Nevado de Huila National Parks (Colombia) and Cayambe-Coca, Cotopaxi and Sangay National Parks (Ecuador). In Río Mazan, a small reserve at the edge of Cajas National Recreation Area (S Ecuador), the species could be threatened by habitat destruction, as remnant patches of forest are gradually being destroyed, although nowadays Río Mazan seems to be well protected. For the conservation of this species in S Ecuador, the effective protection of Cajas National Recreation Area must be ensured.

Bibliography. Best *et al.* (1997), Bloch *et al.* (1991), Butler (1979), Collar *et al.* (1992), Fjeldså & Krabbe (1990), García-Moreno *et al.* (1999), Graves (1980), Gretton (1986), Heindl & Schuchmann (1998), Hilty & Brown (1986), King (1989), Macey *et al.* (1976), Moore (1934b, 1934c, 1940), Salaman & Mazariegos (1998b), Stotz *et al.* (1996), Taylor (1995), Wetmore (1970), Williams & Tobias (1994), Zimmer (1952).

271. Black Metaltail

Metallura phoebe

French: Métallure phébé **German:** Schwarzbauch-Glanzwänzchen **Spanish:** Metalura Negra

Taxonomy. *Ornismya phoebe* Lesson and DeLattre, 1839. Andes of Peru.

Differences in body size and plumage colours have been detected between populations in N Peru and C Peru, but specimens from linking areas require study before division into two races can be considered. Monotypic.

Distribution. Andes of Peru: Pacific slope; in N Peru, E of R Marañón, with single record from W (Jalca de Soquian); and also in C Peru (Huánuco, Junín). Possibly extends into extreme N Chile; two old specimens supposedly from Bolivia.



Descriptive notes. 13-14 cm; 5.6-5.9 g. Male has medium-sized, straight, black bill; body black with rosy grey sheen; glittering turquoise green throat patch; small whitish leg puffs; white spot behind eye conspicuous; moderately forked tail iridescent bronze-gold and rosy grey above, glittering golden orange below. Female similar, but with incomplete throat patch. Immature resembles female but lacks throat patch.

Habitat. Semi-arid open montane scrub and woodland, such as *Polylepis*, vegetated canyons, and bushy and shrubby slopes in the temperate and upper subtropical zone of the Andes. Recorded between 1500 m and 4500 m, but

mostly above 3000 m. Forages mostly in the understory or on the ground.

Food and Feeding. Observed feeding in hover-flight on nectar from a variety of bushes including *Mutisia*, herbs and vines, such as *Cajophora*, *Loasa* and *Salpichroa*, and from smaller flowers like *Ludwigia* in short, matted grass; sometimes in canopy of trees like *Eucalyptus* and *Polylepis* with flowering *Tristerix* mistletoes. Male establishes feeding territories.

Breeding. Eggs laid probably Jul-Dec and Jan. The nest is a pendent mass of moss suspended in roots or from a thin branch overhanging a stream. Clutch size 2; incubation by female. First breeding in second year.

Movements. No information, but presumably sedentary; possibility of seasonal altitudinal movements.

Status and Conservation. Not globally threatened, CITES II. Because pressure of human population is very intense at altitudes of 3250-3800 m on Pacific slope of Peru, only tiny vestiges of fairly undisturbed montane cloudforest remain here. Despite this, the species is still fairly common in many places, including Huascarán National Park and Calpuay National Reserve. However, it is locally threatened by destruction of *Polylepis* woods and vegetational degradation of páramo and jalca grasslands. An additional threat is encroachment into the *Polylepis* woodlands by adaptable and dispersive species. For the preservation of *Polylepis* habitats, fallow-shifting (i.e. alternate periods of agriculture and fallow) has been suggested as a sustainable agricultural practice. Species is thought to occur in Bolivia and Chile, though this has yet to be verified; survey work in the appropriate areas is therefore recommended.

Bibliography. Fjeldså (1992, 1995), Fjeldså & Kessler (1996), Fjeldså & Krabbe (1990), García-Moreno *et al.* (1999), Heindl & Schuchmann (1998), Hughes (1980), Johnson (1967, 1972), Koepcke (1970), Meyer de Schauensee (1982), Olrog (1968), Parker *et al.* (1982), Stotz *et al.* (1996), Zimmer (1930, 1952).

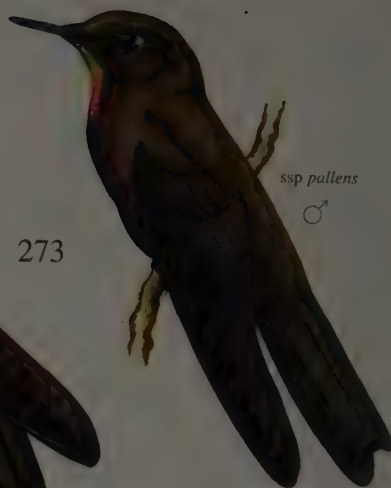


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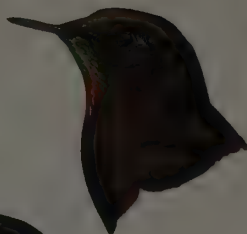
ssp pallens

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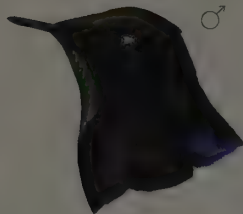
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ssp vulcani

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ssp olivaceum



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ssp versigularis

ssp stanleyi

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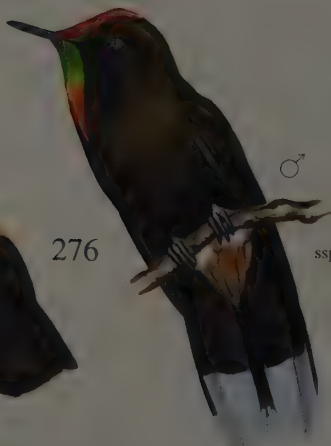


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ssp herrani

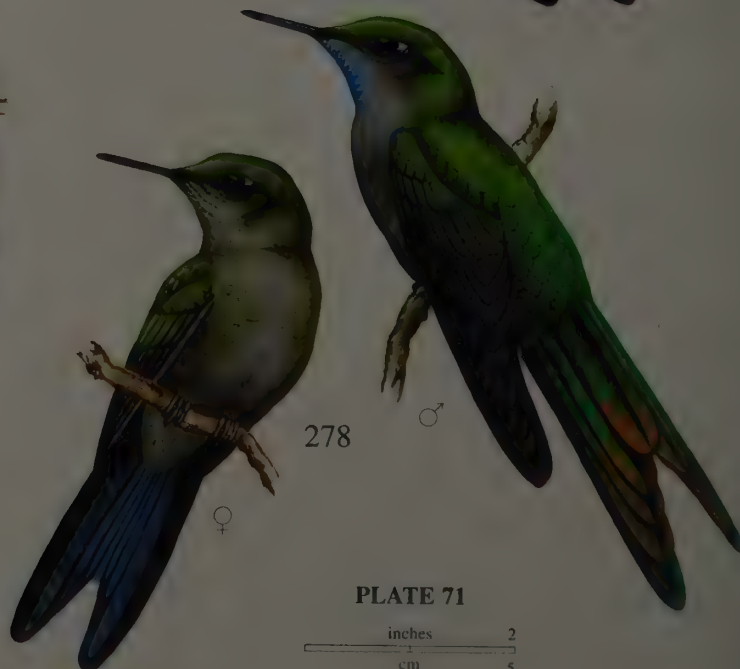


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ssp tolimae



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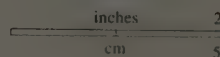


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PLATE 71



Genus *CHALCOSTIGMA* Reichenbach, 1854

272. Rufous-capped Thornbill

Chalcostigma ruficeps

French: Métallure à tête rousse

Spanish: Colibrí Capirrufo

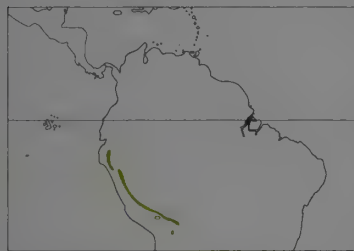
German: Kastanienkappen-Glanzschwänzchen

Other common names: (Rufous-capped) Metalltail

Taxonomy. *Trochilus* (—?) *ruficeps* Gould, 1846, Bolivia.

Previously placed in genus *Metallura*; alternatively separated in monotypic genus *Selatopogon*. Birds of Ecuador have been separated as race *aureofastigiatum*, but this variation has now been demonstrated to form ends of a clinal character progression involving coloration of ornamental throat feathers. Monotypic.

Distribution. E Andes of SE Ecuador through Peru to WC Bolivia (Yungas of Cochabamba). Single record from Pan Azucar in C Andes of Colombia, where status uncertain.



Descriptive notes. 10.5 cm; 3.3–3.9 g. Male has short, straight, black bill; upperparts bottle green, underparts rufous mottled green, especially at sides; crown mahogany red; narrow throat patch emerald green, often grading at lower edge from yellow green through pure yellow into golden yellow; tail dull olive green. Female has throat and breast ochre-orange, dotted with olive green at sides, becoming somewhat paler on belly; outer tail feathers with paler tips. Immature similar to female.

Habitat. From humid second growth and riparian thickets to borders and glades in humid montane forest and moss-laden cloud-

forest. Ranges in altitude from 1400 m to 3500 m, occasionally to 3800 m, but mostly around 2500 m. Forages in low to medium-level strata.

Food and Feeding. Feeds on nectar of Melastomataceae flowers (*Miconia*, *Tibouchina*), *Vallea stipularis* and *Fuchsia canescens*. Sometimes pierces bases of fuchsias and other flowers with long corollas, or uses slits made by flowerpiercers (*Diglossa*). Rarely forages in hover-flight, more often while clinging to inflorescence. Also takes insects. Male establishes feeding territories.

Breeding. Dec-Mar in Bolivia. Enlarged gonads in Aug in Bolivia, Jul-Oct in Peru. Clutch size 2; incubation by female.

Movements. No information; possibly undertakes seasonal altitudinal movements. Individuals recorded at Pan Azucar, in C Andes of Colombia, may indicate migration of some sort.

Status and Conservation. Not globally threatened. CITES II. Generally uncommon. Apparently less sensitive to man-induced environmental changes than other *Chalcostigma* species, since also found in secondary growth and other disturbed habitats. Occurs in the Zona Reservada Apurímac in Peru, and in the Podocarpus National Park in S Ecuador. Research required in C Andes of Colombia, in order to establish whether or not a sedentary population exists.

Bibliography. Best *et al.* (1997), Bloch *et al.* (1991), Bond & Meyer de Schauensee (1943), Butler (1979), Carraker (1935), Fjeldså & Krabbe (1990), Hilty & Brown (1986), Mobbs (1978, 1979), Parker *et al.* (1982), Remsen (1985), Remsen & Traylor (1989), Schuchmann (1978c), Schuchmann & Heindl (1997), Stotz *et al.* (1996), Zimmer (1952).

273. Olivaceous Thornbill

Chalcostigma olivaceum

French: Métallure olivâtre

German: Braunes Glanzschwänzchen

Spanish: Colibrí Oliváceo

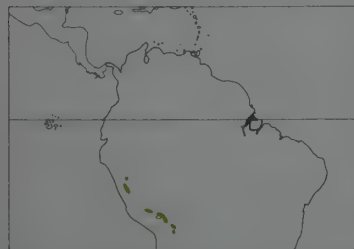
Taxonomy. *Ramphomicon olivaceus* Lawrence, 1864, La Paz, Bolivia.

Two subspecies recognized.

Subspecies and Distribution.

C. o. pallens Carraker, 1935 - locally in Andes of C Peru.

C. o. olivaceum (Lawrence, 1864) - locally in E Andes of SE Peru and WC Bolivia.



Descriptive notes. 14–15 cm; 8–9 g. Male has short, straight, black bill; body uniformly dark olive green; throat patch narrow and emerald green, with elongation (“beard”) grading from yellow through pink into blue-grey or purple-violet distally, with blue-violet tips; tail forked, dull olive green. Female similar, but with incomplete throat patch and reduced “beard”; outer tail feathers with paler tips. Immature similar to female. Race *pallens* smaller and lighter in coloration than nominate.

Habitat. Usually in typical *puna* grassland and cushion plant communities, sometimes in low composite brush, but also at edges of dense

Polylepis-*Gynoxys* woodland. Ranges altitudinally between 3600 m and 4600 m. Forages on the ground and in lower to middle strata.

Food and Feeding. Seen feeding from prostrate red flowers (perhaps *Castilleja*) on boggy slope. Largely insectivorous. Reported to pick up insects from the ground while hopping over densely matted grass and cushion plants, or to probe for insects among the thick mat of hairs covering cushion cacti. Sometimes perches on the ground and darts upwards to catch airborne insects. Male defends feeding territories.

Breeding. Specimens with enlarged gonads found Jan in Bolivia; juveniles seen in Feb-Apr in C Peru and in May around La Paz. Attracted to *Polylepis* patches when breeding. Clutch size 2; incubation by female.

Movements. No information, but presumably sedentary; seasonal altitudinal movements possible.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Peruvian High Andes EBA and High Andes of Bolivia and Argentina EBA. Uncommon and locally distributed. High elevations and inhospitable habitats where this species occurs offer good protection against human interference. nevertheless, studies of ecology and the sensitivity of this relatively unknown hummingbird to man-induced environmental changes are badly needed.

Bibliography. Bond & Meyer de Schauensee (1943), Carraker (1935), Dorst (1956), Fjeldså & Kessler (1996), Fjeldså & Krabbe (1990), Koepcke (1970), Meyer de Schauensee (1982), Mobbs (1978, 1979), Olrog (1968), Parker *et al.* (1982), Remsen & Traylor (1989), Schuchmann & Heindl (1997), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Vuilleumier (1969), Zimmer (1952).

274. Blue-mantled Thornbill

Chalcostigma stanleyi

French: Métallure de Stanley

Spanish: Colibrí de Stanley

German: Schwarzkopf-Glanzschwänzchen

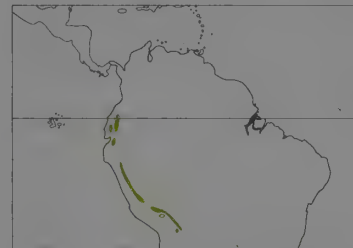
Taxonomy. *Trochilus Stanleyi* Bourcier, 1851, cold regions of Pichincha and Cotopaxi, Ecuador. Three subspecies recognized.

Subspecies and Distribution.

C. s. stanleyi (Bourcier, 1851) - both Andean slopes of Ecuador.

C. s. versigularis Zimmer, 1924 - E Peru in Andes E of R Marañón S to Cordillera Carpi (Huánuco).

C. s. vulcani (Gould, 1852) - S of R Huallaga along E Andes of Peru and WC Bolivia.



Descriptive notes. 12–13 cm; male 6–2 g, female 4–5 g. Male has short, straight, black bill; body dark sooty brown; uppertail-coverts turquoise; crown and nape with bronzy-green, back with violet-blue reflections; throat patch narrow and emerald green, with elongation (“beard”) grading from pink to purple-violet distally, sometimes tipped violet-blue; tail forked, steel blue. Female similar, but throat patch without “beard” and incomplete; outer tail feathers with paler tips. Immature similar to adult female. Race *versigularis* has upperparts completely covered with deeper violet-blue reflections, “beard” with narrower pink

tip; *vulcani* resembles previous race, but elongation of throat patch grades from pink to blue-grey or grey-violet distally.

Habitat. Slopes with rather humid *páramo* and *jalca* vegetation, especially steep and rocky places, where it inhabits small patches of *Gynoxys* or *Polylepis* woodland and scrub. Usually between 3000 m and 4200 m, but occasionally as low as 2200 m. Normally at higher elevations than *C. herrani*. Forages on the ground and in lower strata.

Food and Feeding. Feeds on nectar of small flowers of *Berberis*, *Gauteria*, *Ribes* and a tiny red *Gentiana*. Observed to glean sugary secretions and tiny cicadas and aphids from the undersides of *Gynoxys* leaves while clinging, often with fluttering wings, to the foliage. Picks up insects while hopping on densely matted grass or rocks. Occasionally hawks for airborne insects. Defends feeding territories.

Breeding. Probably breeds during rainy season as juveniles recorded in Mar at La Paz, Bolivia. Clutch size 2; incubation by female.

Movements. The species has been shown to be opportunistic in its altitudinal distribution since it moves to lower elevations during short spells of harsh weather; seasonal altitudinal migration can therefore be expected.

Status and Conservation. Not globally threatened. CITES II. Patchily distributed, but also fairly common. Locally endangered by destruction of *Polylepis* woods and degradation of *páramo* and *jalca* grasslands. An additional threat is the spread into *Polylepis* woodland of adaptable and dispersive bird species. For the preservation of *Polylepis* habitats fallow-shifting (i.e. alternate periods of agriculture and fallow) has been suggested as a sustainable agricultural practice. Occurs in Las Cajas National Recreation Area, Ecuador. Strongly suspected to occur in *páramo* on Volcán Chiles in SE Nariño (SC Colombia), mainly due to sightings just across the border in Ecuador, at Páramo El Angel, in 1982.

Bibliography. Best *et al.* (1997), Bond & Meyer de Schauensee (1943), Butler (1979), Fjeldså (1991, 1993), Fjeldså & Krabbe (1990), Hilty & Brown (1986), Mobbs (1978, 1979), O'Neill & Parker (1978), Parker *et al.* (1982), Remsen & Traylor (1989), Salaman & Mazariegos (1998b), Schuchmann & Heindl (1997), Stotz *et al.* (1996), Todd (1942), Williams & Tobias (1994), Zimmer (1930, 1952).

275. Bronze-tailed Thornbill

Chalcostigma heteropogon

French: Métallure à queue bronzée

Spanish: Colibrí Picoespina

German: Bronzeglanzschwänzchen

Other common names: Bronzy Thornbill

Taxonomy. *Ornismya heteropogon* Boissonneau, 1840, Santa Fé de Bogotá, Colombia.

Monotypic.

Distribution. Extreme W Venezuela (Páramo de Tamá) and E Andes of Colombia (S to Cundinamarca).

Descriptive notes. 13–14 cm; 5.9–6.3 g. Male has short, straight, black bill; upperparts and underparts bottle-green; rump and uppertail-coverts coppery red; throat patch narrow and emerald green, with pink, violet-tipped elongation (“beard”); forked tail olive green. Female similar, but throat pale with darker markings and lacks “beard”; outer tail feathers with paler tips. Immature similar to female, but with mahogany red crown.

Habitat. Semi-arid to humid *páramo*, mainly steep rocky slopes with ferns, bromeliads, shrubs and *Espeletia*, and at the edge of *Polylepis* and other stunted woodland. Ranges altitudinally between 3000 m and 3900 m. Terrestrial foraging, as reported for some members of the genus, has not been noted. Searches for food in lower strata.

Food and Feeding. Feeds on nectar from flowers of *Bartisia santolinaefolia*, *Rubus gachetensis*, *Brachyotum*, *Castilleja fissifolia*, *Hasperomeles* and ericaceous shrubs (*Pernettya*, *Gaultheria*).



Gleans tiny insects from *Espeletia* flowers or from the twigs and leaves of shrubs, while perched below or clinging to the substrate, or in hover-flight. Hawks for flying insects between 1 and 3 m above the ground. After snapping up the prey, the bird tosses it into the air and flies at it with bill open, or tilts its head with open bill backwards to enable the prey to be taken into the rear of the gape. Defends feeding territories.

Breeding. Season probably Sept-Jan, but possibly also at other times. Female in breeding condition with 2 juveniles recorded late Jul in NE Colombia. Clutch size 2; incubation

by female.

Movements. No information, but presumably sedentary; possibly makes seasonal altitudinal movements.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Colombian East Andes EBA. Generally uncommon. The introduction of unsustainable land-use practices, such as ploughing downhill, increased use of fire, and a shift from camelids to sheep, has led to severe degradation of the *Polylepis* woodlands. However, the altitude and inhospitable climate of the region inhabited by present species offer some protection against intrusion by man. Parts of range are under official protection, such as the Sumapaz National Park in Colombia, and the Tamá National Park on the border with Venezuela.

Bibliography. Fjeldsá & Krabbe (1990), Hilty & Brown (1986), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978, 1979), Olog (1968), Schuchmann & Heindl (1997), Snow (1983), Stattersfield *et al.* (1998), Stotz *et al.* (1996).

276. Rainbow-bearded Thornbill

Chalcostigma herrani

French: Métallure arc-en-ciel

Spanish: Colibrí de Herrán

German: Weißspitzen-Glanzschwänzchen

Other common names: Herran's Thornbill

Taxonomy. *Trochilus Herrani* DeLattre and Bourcier, 1846, Pasto, Colombia.

In past, sometimes separated in monospecific genus *Eupogonius*. Two subspecies recognized.

Subspecies and Distribution.

C. h. tolimae Kleinschmidt, 1927 - Volcán Tolima in C Andes of Colombia.

C. h. herrani (DeLattre & Bourcier, 1846) - W Andes of Colombia (Munchique to Nariño) through both slopes in Ecuador to N Peru (Piura).



Descriptive notes. 10-12 cm; male 6-4 g, female 5-5 g. Male has short, straight, black bill; upperparts and underparts bottle green; rump and uppertail-coverts coppery red; forehead rufous, crown almost black, with light rufous stripe centrally; throat patch emerald green, with glittering fiery red elongation, feathers of which spread out over breast; rounded tail blue-violet, broadly tipped white. Female similar, but forehead and crown only rufous; throat patch incomplete and elongation lacking or reduced. Immature similar to female. Race *tolimae* darker green; throat patch and elongation form a narrow "beard".

Habitat. Usually below actual páramo; on well-drained rocky slopes with ferns, bromeliads and various shrubs. Sometimes in humid *Polylepis* woods in páramo. Ranges altitudinally mostly between 2700 m and 3600 m, to around 4000 m on Volcán Tolima. Replaced at higher elevations by *C. stanleyi* in true páramo habitats. Forages on the ground and in low to middle strata.

Food and Feeding. Feeds hovering on nectar from flowers of *Brachyotum* and *Puya*, often clinging to them while feeding. Gleans insects from leaves or bark in higher vegetation strata, as well as from low plants and tussocks of grass while hopping on or close to the ground. Takes prey in bill tip and tosses it into the air, then either flies at it with bill open or tilts head backwards with bill open to get prey into the rear of the gape. Defends feeding territories.

Breeding. 2 nests with eggs found Sept on Páramo del Tábano at 3000 m. Nest-building female observed mid-Jul at Mt Sangay, Ecuador, at 4000 m; nest placed in niche of perpendicular cliff, about 7 m above water, among ferns and hanging vines. Clutch size 2; incubation by female.

Movements. No information, but presumably sedentary; possibly makes seasonal altitudinal movements.

Status and Conservation. Not globally threatened. CITES II. Common in W Colombia and in N Peru. Found in Podocarpus National Park and Las Cajas National Recreation Area, in S Ecuador; Cotopaxi National Park, SE of Quito; and Puracé National Park, in S Colombia. Most of the Podocarpus National Park was open to gold mining until 1993; when concession lifted due to international campaign, only a small part had been mined; casual gold prospectors and settlers, who had already established some dwellings and small-scale logging concerns inside the park, are now pushing for access, and pressure is likely to increase greatly in future.

Bibliography. Best *et al.* (1997), Bloch *et al.* (1991), Borrero (1947), Butler (1979), Collar & Andrew (1988), Fjeldsá & Krabbe (1990), Graves (1980), Hilty & Brown (1986), Mobbs (1978, 1979), Moore (1934c), Parker, Parker & Plenge (1982), Parker, Schulenberg *et al.* (1985), Ridgely (1980), Salaman & Mazariegos (1998b), Schuchmann & Heindl (1997), Stotz *et al.* (1996), Vélez & Velázquez (1998), Zimmer (1952).

Genus *OPISTHOPRORA* Cabanis & Heine, 1860

277. Mountain Avocetbill

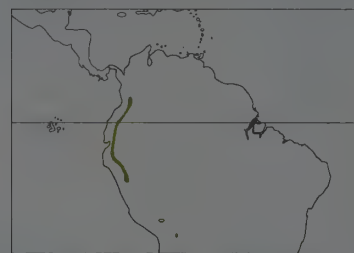
Opisthoprora euryptera

French: Colibri avocettin **German:** Fleckenbauch-Avosettkolibri **Spanish:** Colibrí Picolezna
Other common names: Loddiges Thornbill, Avocetbill

Taxonomy. *Trochilus eurypterus* Loddiges, 1832, Popayán, Colombia.

Little known species with uncertain systematic affinities. Monotypic.

Distribution. Colombia (C Andes from Caldas to SE Nariño) through E Ecuador to N Peru (Amazonas to La Libertad).



Descriptive notes. 9-10.2 cm; male 6-4-6-8 g, female 5-8-6-2 g. Male has short black bill, upturned at tip. Upperparts shining green, coppery on crown and sides of head; small white postocular spot; underparts white, streaked dark green, buff on belly; central tail feathers green, rest bluish-black with narrow white tips. Female similar to male. Immature like adult but head and neck feathers have brown fringes.

Habitat. Forest borders and open shrubby slopes of sub-páramo and páramo from 2600 m to 3600 m, in Ecuador most numerous at 2900-3300 m; forages low down, at 1-4 m, often clinging to flowering Ericaceae.

Food and Feeding. Nectar of flowering Ericaceae, Onagraceae (especially *Fuchsia*), Rubiaceae, Lobeliaceae. Insects are caught in the air by hawking.

Breeding. Unknown. Gonadal activity indicates season Jan-Apr.

Movements. Sedentary, but altitudinal dispersal may occur.

Status and Conservation. Not globally threatened. CITES II. Rare to uncommon throughout range. Fairly numerous in some areas of NW Ecuador. Present species should be carefully monitored in the future, since its mountain habitat, particularly in Colombia, is relatively suitable for agriculture and cattle-raising. Regularly recorded in Puracé National Park, Colombia.

Bibliography. Baez *et al.* (1997), Best *et al.* (1997), Butler (1979), Fitzpatrick & Willard (1982), Fjeldsá & Krabbe (1986, 1990), Hilty & Brown (1986), Meyer de Schauensee (1982), Olog (1968), Parker, Parker & Plenge (1982), Parker, Schulenberg *et al.* (1985), Rahbek *et al.* (1995), Salaman & Mazariegos (1998b), Stotz *et al.* (1996), Taylor (1995).

Genus *TAPHROLESBIA* Simon, 1918

278. Grey-bellied Comet

Taphrolesbia griseiventris

French: Colibri comète

German: Graubauchsylphe

Spanish: Colibrí Ventrigrís

Other common names: Grey-breasted Comet

Taxonomy. *Cynanthus griseiventris* Taczanowski, 1883, Paucal, Peru.

Uncertain systematic position; probably closest to *Polyommus* and *Sappho*. Monotypic.

Distribution. NW Andes of Peru (S Cajamarca to W Huánuco).



Descriptive notes. 14-17 cm (including bill 2-2 cm and tail up to 8-5 cm). Male has straight black bill; upperparts bronzy-green, postocular spot white; underparts light grey with blue throat; tail long, deeply forked, bottle green to golden-orange at tips of rectrices. Female similar to male but lacks blue throat; tail shorter and less forked. Immature similar to adult but throat and breast tawny.

Habitat. Bushy semi-arid areas with scattered trees or thickets in canyons, partly cultivated hillsides, at 2600-3500 m.

Food and Feeding. Has been recorded taking nectar of flowering cacti, *Agave*, Amaryllidaceae and *Puya*.

Breeding. No information available.

Movements. Presumably sedentary.

Status and Conservation. VULNERABLE. CITES II. Restricted-range species; present in Marañón Valley EBA and Peruvian High Andes EBA. Generally rather rare. In its very limited distribution, no threats have been identified to date. Habitat preferences suggest acceptance of disturbed areas to some extent. Recent records in the upper Marañón Valley, near Cajabamba, Paucal and Culcui.

Bibliography. Baron (1897), Bond (1954), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Fjeldsá & Krabbe (1990), Inskipp (1987), Parker *et al.* (1982), Plenge (1979), Simon (1919, 1921), Stattersfield *et al.* (1998), Stephens & Traylor (1983), Stotz *et al.* (1996), Wege & Long (1995), Zimmer (1930, 1952).



Genus *AGLAIOCERCUS* Zimmer, 1930

279. Long-tailed Sylph

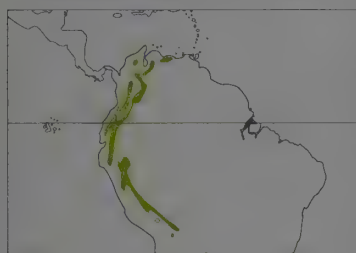
Agelaiocercus kingi

French: Sylphe à queue d'azur **German:** Himmelssylphe **Spanish:** Silfo de King
Other common names: Green-tailed/Green-throated/Emma's Sylph (*emmae*); Blue-throated Sylph (*kingi*)

Taxonomy. *Trochilus kingi* Lesson, 1832, Jamaica; error = Bogotá, Colombia. Genus name formerly given as *Cyanolesbia*, but this is not applicable. Forms a superspecies with *A. coelestis* and *A. berlepschi*; both of these have sometimes been considered conspecific with present species, but notable differences in morphology and range, especially altitudinal, indicate that separate species status is more appropriate; evidence suggests hybridization very limited in areas of contact. Race *emmae* has also been considered a separate species, usually incorporating *caudatus* or *mocoa*, or both, as races. Forms described as "*Chalcostigma purpureicauda*" and "*Zodalia thaumasia*", both known only from single specimens, are apparently hybrids of present species and *Lesbia victoriae*; "*Neolesbia nehrkorni*" is known from only two specimens and appears to be a hybrid of present species with *Ramphomicron microrhynchum*, or perhaps with *Thalurania furcata* or *T. colombica*. Six subspecies currently recognized.

Subspecies and Distribution.

A. k. margarethae (Heine, 1863) - NC and coastal Venezuela.
A. k. caudatus (Berlepsch, 1892) - W Venezuela and N Colombia.
A. k. emmae (Berlepsch, 1892) - C Andes of N Colombia to W Andes of S Colombia and NW Ecuador.
A. k. kingi (Lesson, 1832) - E Andes of Colombia.
A. k. mocoa (DeLattre & Bourcier, 1846) - C Andes of S Colombia, Ecuador and N Peru.
A. k. smaragdinus (Gould, 1846) - E Andes of Peru and WC Bolivia.



Descriptive notes. Male 16-19 cm (including outer tail feathers 12 cm), 5-6 g; female 9-11.7 cm, c. 4-7 g. Male has short black bill; upperparts glittering, bronzy metallic green, underparts slightly duller, olive; crown shining emerald green, dark green towards back of head; small throat patch either blue or violet; tail iridescent blue, green and violet above, bluish-black below, central tail feathers very short, outer ones extremely long. Female similar to male but underparts cinnamon as well as metallic green; head metallic green; throat buffy or white and spotted green, short white malar streak; tail narrow, short and forked;

outer tail feathers dark blue, broadly tipped white. Immature similar to adult female but slightly buffy below, diffusely spotted green, and with concealed white patch on lower back. Race *margarethae* is paler green on upperparts than nominate, female similar to nominate; *caudatus* lacks blue throat spot, tail purple-blue, female like nominate; *emmae* has longer bill, plumage paler and duller green, throat bright green, female with more green spots on whitish throat; *mocoa* is more glittering green above, throat sapphire blue to purple, female like nominate; *smaragdinus* has shorter tail, throat spot greenish-blue, female is bronzy green on upperparts, crown more bluish-green, has chestnut wash on back and green discs on throat.

Habitat. Variable, depending on location of population and time of year. Pre-montane zones, scrubland and clearings, gardens, occasionally grassland and edges of humid forest and second-growth woodland, but rarely in forest interior; occurs from 900 m up to 3000 m.

Food and Feeding. Nectar and insects. Engages in a variety of forms of feeding behaviour, including trap-lining, territorial defence, and nectar robbing by means of piercing base of flower corolla. Hovers at flowers but may also perch on them in order to feed. Hawks for insects from a perch. In pre-montane zones, species feeds primarily in tree tops, and will occasionally feed with other hummingbirds in flowering trees. Feeds at small shrubs and trees in elfin forest and likewise in areas of high-altitude grassland.

Breeding. Feb-Oct recorded, but species thought to breed throughout the year. Male engages in ritualized nest building. Bulky, domed nest has a side entrance and is made of moss and plant fibres; attached to twig or branch and somewhat hidden by leaves. Female may sleep in nest every night. Lays 2 eggs; incubation 15-17 days, by female; fledging 21-24 days.

Movements. Andean populations undergo seasonal altitudinal migrations from pre-montane zone to higher regions around 2500-2700 m, occasionally up to 3000 m. Populations in W Venezuela (*caudatus*) may migrate to N Colombia. At La Planada Reserve, Nariño (SW Colombia), in zone of contact with *A. coelestis*, present species is seasonally dominant, but is apparently driven out by its congener during dry season, Jan-Apr.

Status and Conservation. Not globally threatened. Common throughout moderate elevations of E & C Andes and in parts of lowland Venezuela. In Venezuela, abundant in montane forest regions of Sierra Nevada National Park, Mérida, as well as in plantations nearby; relatively common at borders of secondary vegetation around Colonia Tovar, near Caracas; also common in Henri Pittier National Park, Aragua, where regularly visits feeders at Rancho Grande Biological Station. In Colombia, common along edges of montane forests below Chingaza National Park and in city parks of Bogotá when *Eucalyptus* is in flower; at La Planada Reserve, local densities of at least 2-3 pairs/km² have been recorded. In Ecuador, common resident in forest patches below Porculla Pass. Habitat destruction in Colombia and Ecuador, due to cattle-raising, may be affecting native flora in such a way as to cause a decrease in food plants; this could present a threat to the species.

Bibliography. Best *et al.* (1997), Bloch *et al.* (1991), Bond & Meyer de Schauensee (1943), Butler (1979), Davies *et al.* (1994), Fjeldså & Krabbe (1990), Hilty & Brown (1986), Hinkelmann *et al.* (1991), Meyer de Schauensee & Phelps (1978), Miller (1963), Parker *et al.* (1982), Rensen & Traylor (1989), Rensen, Traylor & Parkes (1986), Ridgely & Gaulin (1980), Ruschi (1961d, 1973b), Rutgers & Norris (1972), Salaman & Mazariegos (1998b), Schuchmann & Duffner (1993), Snow & Snow (1980), Stotz *et al.* (1996), Taylor (1995), Wetmore (1939), Williams & Tobias (1994), Zimmer (1930).

280. Violet-tailed Sylph

Agelaiocercus coelestis

French: Sylphe à queue violette **German:** Langschwanzsylphe **Spanish:** Silfo Celeste

Taxonomy. *Cyananthus coelestis* Gould, 1861, Ecuador.

Genus name formerly given as *Cyanolesbia*, but this is not applicable. Forms a superspecies with *A. kingi* and *A. berlepschi*. Formerly treated as a race of *A. kingi*, but morphology and range, especially altitudinal distribution, indicate species status more apt; female notably different from that of *A. kingi*. Proposed race *pseudocoelestis* best considered synonymous with nominate, since morphological differences are superficial. Two subspecies currently recognized.

Subspecies and Distribution.

A. c. coelestis (Gould, 1861) - Pacific slope of W Andes of both Colombia and N & C Ecuador.
A. c. aethereus (Chapman, 1925) - SW Ecuador, S from Zaruma.



Descriptive notes. Male 18-21 cm (including outer tail feathers 10-15 cm), female 9.5-9.7 cm; 4.6-5.2 g. Male has short, straight, black bill; crown and back shining green becoming violet-blue on rump, small postocular spot buffy white; gorget violet-blue, rest of underparts green; tail elongated, deeply forked, mostly iridescent metallic violet, tipped blue. Female has crown glittering blue, postocular spot whitish; throat white with green spots, band across chest white, rest of underparts cinnamon-rufous; tail short, unforked, bluish-green, with outer rectrices tipped white. Immature dull green above, buffy green below.

head feathers with buffy fringes. In race *aethereus*, male has gorget green, female less heavily spotted on throat.

Habitat. Cloudforest, forest borders, semi-open terrain with shrubs and stands of trees, at 1000-2000 m, occasionally much lower, most numerous around 1000 m. Forages from near ground occasionally up to tree tops, along edges and trails and inside forest. Male and female trap-line along clumps of dispersed flowers; male occasionally defends feeding territory.

Food and Feeding. Nectar of flowering vines, shrubs and trees, including *Bomarea*, *Clusia*, Ericads, bromeliads and *Inga*. Often clings to corolla while feeding. Insects are caught in the air by hawking, or gleaned from vegetation.

Breeding. Oct-Feb. Domed nest with side entrance is built from moss and spider webs in clumps of moss or epiphytes. Clutch 2; incubation 15-17 days, by female; chick pale-coloured with sparse greyish dorsal down; fledging at 26-30 days. Male and female build nests outside the reproductive period where they roost at night; this may have misled ornithologists to assume breeding activity almost all year round.

Movements. Sedentary, with some local altitudinal dispersal depending on flowering season. At La Planada Reserve, Nariño (SW Colombia), in zone of contact with *A. kingi*, present species is dominant in dry season, Jan-Apr, numbers declining during wet season.

Status and Conservation. Not globally threatened. Common resident of cloudforest. The species will tolerate areas of man-made habitats as long as patches of forest remain. Several national parks within the distributional range of the species provide adequate protection for local populations. In Colombia, common resident at edges of cloudforest of Los Farallones National Park, near Cali, with local densities of at least 3-4 pairs/km²; at La Planada Reserve, density varies from at least 5-7 pairs/km² in dry season to at least 2 pairs/km² in wet season; also recorded in Rio Nambi Reserve.

Bibliography. Best, Checker *et al.* (1996), Best, Heijnen & Williams (1997), Bloch *et al.* (1991), Butler (1979), Chapman (1925a), Fritsch & Schuchmann (1988), Hesse & Hesse (1982), Hilty (1997), Hilty & Brown (1986), Kleefisch (1980), Peikert (1983), Salaman (1996), Salaman & Mazariegos (1998b), Schuchmann (1989), Schuchmann & Duffner (1993), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Taylor (1995), Williams & Tobias (1994).

281. Venezuelan Sylph

Agelaiocercus berlepschi

French: Sylphe du Venezuela **German:** Berlepschsylphe **Spanish:** Silfo de Berlepsch

Taxonomy. *Cyanolesbia berlepschi* Hartert, 1898, Cumaná, Venezuela.

Genus name formerly given as *Cyanolesbia*, but this is not applicable. Forms a superspecies with *A. kingi* and *A. coelestis*; these three species may be parapatric in some parts of their ranges but hybridization does not appear to be common. Present species has been treated as a race of *A. kingi* by several authors, but based on morphological distinctions and isolation of the population it is best considered a separate species; female strikingly different. Has alternatively been considered a race of *A. coelestis*, although this would appear difficult to justify. Monotypic.

Distribution. NE Venezuela: E coastal Cordillera de la Costa in Sucre, and Cerro Negro in Monagas.



Descriptive notes. Male 22 cm (including outer tail feathers 14-15 cm), 5.5 g; female 9.5-11 cm, 4.5 g. Male has short black bill; upperparts shining green with a darker glittering green crown; underparts bronzy-green, with glittering blue gorget; thigh feathers puffy white; outer tail feathers extremely long and broad, basally deep violet, distally blue, central tail feathers shorter and blue-green. Female shining green above with glittering blue crown; throat, breast and belly mostly white, sides bronzy-green; tail slightly forked, blue-green, outer feathers tipped white and considerably shorter (only 4 cm) and narrower than in male.

Immature similar to adult female but head feathers fringed buffy.

Habitat. Coastal slopes, scrub and forest habitats in subtropical montane zone from 1450 m to 1800 m.
Food and Feeding. Nectar of flowering shrubs, vines and trees, especially *Inga*. Forages alone or in pairs from low underbrush to highest tree tops, favouring forest borders and more open habitat.

Either trap-lines or defends territories. Flycatches from perch. Sometime aggregates with other hummingbirds.

Breeding. Aug-Jan. Domed nest is built in epiphytes. All nest building and incubation of eggs is performed by female. No further information.

Movements. Sedentary.

Status and Conservation. Not globally threatened. Population biology is poorly known. Locally abundant within its very small range in the mountains of NE Venezuela N of R Orinoco and extending to near the coast; occurs within Península de Paria National Park, of which the core area is reasonably well protected.

Bibliography. Meyer de Schauensee & Phelps (1978), Phelps & Phelps (1958), Schuchmann & Duffner (1993), Zimmer (1952).

Genus *AUGASTES* Gould, 1849

282. Hyacinth Visorbearer

Augastes scutatus

French: Colibri superbe **German:** Grünmaskenkolibri **Spanish:** Colibri Colaceleste

Taxonomy. *Trochilus scutatus* Temminck, 1824, Brazil.

Affinities of genus unknown; song and nest pattern indicate relationship with *Colibri*. Race *soaresi* is sometimes considered intermediate between nominate and *ilseae*. Three subspecies recognized.

Subspecies and Distribution.

A. s. scutatus (Temminck, 1824) - high altitudes in mountainous parts of C & E Minas Gerais (EC Brazil).

A. s. ilseae Grantsau, 1967 - moderate altitudes in mountainous parts of C & E Minas Gerais (EC Brazil).

A. s. soaresi Ruschi, 1963 - R Paricicaba basin in SC Minas Gerais (EC Brazil).



Descriptive notes. 8.3-9.7 cm; 3.5-5 g. Male has short, straight, black bill; crown and rest of upperparts bronze-green, postocular spot white, forehead and throat shining golden green, edged black, ruff at sides of neck purplish-blue, pectoral band creamy white, belly deep blue; tail iridescent bronzy-green. Female similar to male, black border to the green of crown lacking, belly blue mottled with grey and blue-green; colour of rectrices similar to male but outer ones tipped grey. Immature similar to adult female, but lacks glittering throat plumage; belly grey; immature male has blue sides to neck. Race *ilseae* with dark vio-

let on sides of neck, belly violet-blue, rectrices bluish-green below; *soaresi* has blue line between violet and black plumage on sides of neck, generally larger than other races.

Habitat. Montane regions with xerophytic vegetation and in ravines with dense montane forest between 900 m and 2000 m, commonest at 1000-1600 m; forages at 2-3 m above ground. Two races show altitudinal segregation: *ilseae* typically occurs in gallery forests and bushy areas around c. 900 m, but up to c. 1200 m; nominate occupies rocky areas with low vegetation at higher altitudes, up to c. 2000 m.

Food and Feeding. Nectar of flowering terrestrial bromeliads, cacti, Lorantheae, Verbenaceae, Velloziaceae and Vochysiaceae. Hawks for insects in the air.

Breeding. Nesting females recorded in Jan, Feb and Jul. The small, cup-shaped nest is built of Compositae seeds, cactus wool, etc., and has fragments of dry leaves attached with spider web to the outer wall; placed in exposed vertically forked branches, 0.6-2 m above the ground. Clutch size 2; incubation 15-16 days, by female; fledging period 19-23 days.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Currently considered Near-threatened. Restricted-range species; present in Central Brazilian Hills and Tablelands EBA. Locally common. Habitat is considered relatively safe since unsuitable for agricultural purposes. Occurs in Serra do Cipó National Park (Minas Gerais).

Bibliography. Berlioz (1964), Collar & Andrew (1988), Forrester (1993), Grantsau (1967, 1968b, 1988), Ruschi (1962a, 1963a, 1981-1982, 1982a, 1986), Sazima (1977), Sazima & Sazima (1990), Sick (1993, 1997), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Tobias *et al.* (1993), Willis (1992).

283. Hooded Visorbearer

Augastes lumachella

French: Colibri lumachelle **German:** Goldmaskenkolibri **Spanish:** Colibri Lumaquela

Taxonomy. *Ornismya lumachella* Lesson, 1838, Bahia, Brazil.

Affinities of genus unknown; song and nest pattern indicate relationship with *Colibri*. Species name often erroneously given as *lumachellus*, but original word comes from Italian and thus invariable in scientific nomenclature. Monotypic.

Distribution. Montane plateaux of Brazil (NE & C Bahia, Minas Gerais).



Descriptive notes. 9-10 cm; 4-4.8 g. Male has short, straight, black bill; crown and sides of throat velvet black, forehead and throat iridescent golden green, glittering golden to fiery red at the base of the throat, pectoral white band, white postocular spot; rest of body plumage bronze-green; tail feathers coppery red. Female similar to male but with sides of head brown. Immature similar to adult female with sides of head greyish.

Habitat. Occurs in plateau regions with cacti and scattered small xerophytic shrubs from 900 m to 2000 m, most numerous at 1000 m; forages low down, often below 1 m.

Food and Feeding. Nectar of flowering cacti, terrestrial bromeliads, Rubiaceae, Myrtaceae and Lorantheae. Insects taken in the air by hawking.

Breeding. Jan-May. The tiny cup-shaped nest of soft Compositae seeds and cacti wool, decorated on outer wall with moss held together by spider web, is built in exposed, dry, vertically forked branches, 0.6-0.8 m above the ground. Clutch size 2; incubation 15-16 days, by female; fledging period 20-24 days.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Currently considered Near-threatened. Restricted-range species; present in Central Brazilian Hills and Tablelands EBA. Locally common. Habitat is considered relatively secure, since unsuitable for agricultural purposes.

Bibliography. Berlioz (1944), Forrester (1993), Grantsau (1967, 1968b, 1988), Greenway (1967), Ruschi (1962a, 1963a, 1981-1982, 1982a, 1986), Sargeant (1996), Sick (1993, 1997), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Willis (1992).

284. Wedge-billed Hummingbird

Augastes geoffroyi

French: Colibri de Geoffroy **German:** Bunthalskolibri **Spanish:** Colibri Picocuña

Taxonomy. *Trochilus Geoffroyi* Bourcier, 1843, Cauca Valley, near Cartagena, Colombia; error = La Roble, Colombia.

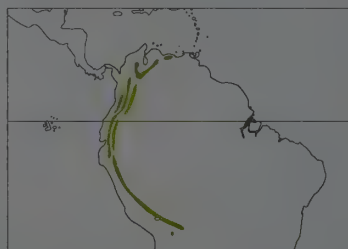
Affinities of genus unknown; song and nest pattern indicate relationship with *Colibri*. Species commonly separated in monotypic genus *Schistes*, but external morphology and behaviour indicate placement in *Augastes*. Race *albugularis* sometimes considered a separate species; however, as zone of introgression in W Ecuador has not yet been studied, this form probably best maintained as race for the present. Type specimen of proposed race "*bolivianus*" (Bolivia) does not match existing population of Bolivia, and may be an artefact of nominate and *albugularis*. Three subspecies recognized.

Subspecies and Distribution.

A. g. geoffroyi (Bourcier, 1843) - N Venezuela through E Colombia and E Ecuador to E Peru.

A. g. albugularis (Gould, 1851) - W Colombia (W Andes and W slope of C Andes) to W Ecuador.

A. g. chapmani (Berlioz, 1941) - C Bolivia (Cochabamba).



Descriptive notes. 8.6-9.3 cm; 3.5-4.1 g. Male has short straight bill, broad at base, sharply pointed, black; above bronzy-green becoming coppery on rump; throat iridescent golden green, broken pectoral band white, patch on each side of throat glittering violet, rest of underparts green, undertail coverts white; tail rounded, central rectrices green, rest bronze green with darkish blue subterminal band, tipped white. Female similar to male, but gorget duller. Immature probably similar to adult female. Race *albugularis* similar to nominate, but lateral throat patches more violet-blue, white pectoral band extends unbroken across chest, lower back and central rectrices dark green, undertail coverts shining bronze green, female has throat white like pectoral band, glittering forehead lacking, patch at side of throat mainly blue; *chapmani* has uniform coloured crown like nominate, lateral throat patches without white, less white on belly.

Habitat. Occurs in dense cloudforests and forest borders between 900-2500 m. In the W Andes of Colombia most numerous between 1500-2000 m; forages at low to medium heights in dense vegetation.

Food and Feeding. Nectar of flowering shrubs, vines and small trees, e.g. *Centropogon*, *Psammisia*, *Cavendishia*, *Palicourea*, *Besleria*. Insects are caught in the air by hawking, occasionally collected from plant surface.

Breeding. Season Aug-Nov. Cup-shaped nest of soft woolly seed fibre of bromelids, cacti and grass, and is fixed with spider web, decorated with lichen on the outer wall, c. 2 m above the ground. Clutch size 2; incubation 15-16 days, by female; fledging 20-22 days.

Movements. Sedentary with some altitudinal dispersion after the breeding season.

Status and Conservation. Not globally threatened. CITES II. Uncommon to locally common in dense cloudforest. Occurs in Henri Pittier National Park (Venezuela). Particularly common in cloudforest above Cali, Colombia, with at least 3-4 pairs/km².

Bibliography. Berlioz (1968), Best *et al.* (1997), Butler (1979), Davies *et al.* (1994), Fjeldså & Krabbe (1990), Hilty (1985), Hilty & Brown (1986), Meyer de Schauensee & Phelps (1978), Miller (1963), Parker *et al.* (1982), Remsen & Taylor (1989), Renjifo *et al.* (1997), Ridgely & Gaulin (1980), Ruschi (1963a, 1964b, 1981-1982), Salaman & Mazariegos (1998b), Stotz *et al.* (1996), Taylor (1995), Todd (1942), Williams & Tobias (1994), Zimmer (1953a).



Genus *HELIOTHRYX* Boie, 1831

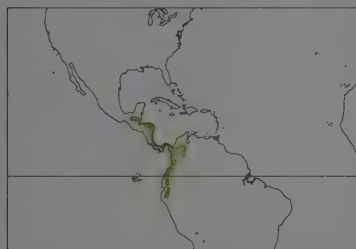
285. Purple-crowned Fairy

Heliothryx barroti

French: Colibri féérique **Spanish:** Colibrí Hada Occidental
German: Purpurkron-Schmuckkolibri
Other common names: Barrot's Fairy

Taxonomy. *Trochilus Barroti* Bourcier, 1843, Cartagena, Colombia.

Forms superspecies with *H. aurita*, with which sometimes regarded as conspecific; a narrow zone of distributional overlap exists in NW Colombia, but both taxa maintain their distinctness. Monotypic. **Distribution.** SE Mexico (E Tabasco, NE Chiapas) and Belize S on Caribbean slope to Nicaragua, then both slopes of Costa Rica and Panama through W Colombia (E to lower and middle Magdalena Valley, S to N Caldas) to SW Ecuador (El Oro).



Descriptive notes. 11-13 cm; 5-5.7 g. Male has short straight bill, sharply pointed, black; forehead iridescent violet, subocular band black, glittering purple on ear-coverts, rest of upperparts shining green; underparts white; rectrices rounded, outer feathers white, central pair darkish blue. Female similar to male, crown green, rectrices markedly longer than male's, with black band at base. Immature similar to female but feathers on head with cinnamon fringes and throat with fine greyish spots. **Habitat.** Occurs in wet lowland forests, at forest edges and in second growth from sea-level to 1000 m, most numerous below 500 m; birds

at higher altitudes are not engaged in breeding. Forages from ground to tree tops.

Food and Feeding. Nectar of flowering vines, epiphytes, shrubs and trees, such as *Passiflora*, *Guzmania*, *Cavendishia*, or *Erythrina*. Often reaches nectar by piercing the corolla base. Insects are caught in the air by hawking.

Breeding. Jan-May, occasionally to Jun. Cup-like, cone-shaped, and laterally attached nest is built in vines or dead twigs, and consists mainly of seed down held together by spider web, 4-8 m above the ground, occasionally higher. Clutch size 2; incubation 16-17 days, by female; chick is black with some greyish dorsal down; fledging at 20-24 days. First breeding in second year.

Movements. Sedentary, but with seasonal dispersal to upper tropical forest zone.

Status and Conservation. Not globally threatened. CITES II. Common in lowlands and foothills throughout range. Occurs in several protected areas such as Manuel Antonio, Braulio Carrillo and Corcovado National Parks (Costa Rica) and Los Katios National Park and Río Nambi Reserve (Colombia). In Anchicayá Valley near Buenaventura (W Colombia), densities of at least 2-3 pairs/km². **Bibliography.** Álvarez del Toro (1980), Berlioz (1954, 1971b), Berret (1963), Best *et al.* (1997), Blake (1958), Butler (1979), Fogden (1993), González-García (1993), Haffer (1967), Hilty (1997), Hilty & Brown (1986), Howell, S.N.G. & Webb (1995a), Howell, T.R. (1957), Land (1970), McDade & Kinsman (1980), Miller (1995), Monroe (1968), Nosedal (1981), Pople *et al.* (1997), Ridgely & Gwynne (1989), Schuchmann (1990c), Skutch (1961b), Slud (1964), Smithe (1966), Stiles (1980, 1985c, 1995b), Stiles & Skutch (1989), Stotz *et al.* (1996), Vleck (1981), Wetmore (1968a), Williams & Tobias (1994), Willis & Eisenmann (1979), Zimmer (1953a).

286. Black-eared Fairy

Heliothryx aurita

French: Colibri oreillard **Spanish:** Colibrí Hada Oriental
German: Schwarzohr-Schmuckkolibri
Other common names: Green-chinned Fairy

Taxonomy. *Trochilus auritus* J. F. Gmelin, 1788, Cayenne.

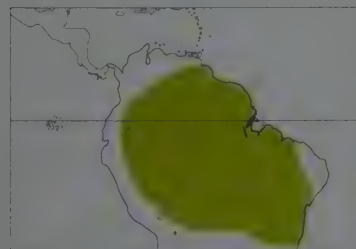
Forms superspecies with *H. barroti*, with which sometimes regarded as conspecific; a narrow zone of distributional overlap exists in NW Colombia, but both taxa maintain their distinctness. Proposed race *major* of present species is most likely a young male of *H. barroti*. Three subspecies recognized.

Subspecies and Distribution.

H. a. aurita (J. F. Gmelin, 1788) - SE Colombia and E Ecuador through N Brazil (N of Amazon) to NE Venezuela (E Sucre) and the Guianas.

H. a. phainolaema Gould, 1855 - NC Brazil (S of Amazon in Pará and Maranhão).

H. a. auriculata (Nordmann, 1835) - E Peru and C Bolivia to C & E Brazil (Amazonia S of Amazon through Mato Grosso to Alagoas and Bahia, and S to Espírito Santo, irregularly to Santa Catarina).



Descriptive notes. 10-13.7 cm; 5-6.3 g. Male has short straight bill, sharply pointed, black; crown glittering green, subocular band black, ear-coverts glittering purple, rest of upperparts shining green; underparts white; tail rounded, outer three rectrices white, two central ones darkish blue. Female similar to male, glittering purple ear-coverts lacking; throat and breast with greyish dots; tail longer than that of male, outer three rectrices white with basal black band. Immature similar to adult female, feathers on head and neck with cinnamon fringes. Male of race *phainolaema* has chin and throat green (much individual variation), female immaculate white below; male of race *auriculata* has green on chin and sides of throat.

Habitat. Wet lowland forest, forest edges and secondary growth up to 800 m, commonest below 400 m; forages from middle strata to tree tops inside forest.

Food and Feeding. Nectar of flowering shrubs, vines, cacti, epiphytes and trees, including Rubiaceae, Rutaceae, Zingiberaceae, Passifloraceae and Leguminosae. Also feeds by flower piercing. Catches insects in the air by hawking.

Breeding. All year round, mainly Jul-Mar. Nest downy cup, attached to a vertical branch, 3-30 m above the ground. Clutch size 2; incubation 15-16 days, by female; chick black with sparse greyish dorsal down; fledging period 23-26 days. First breeding in second year.

Movements. Generally sedentary, though reports of irregular occurrence in S Brazil might be related to movements of some sort.

Status and Conservation. Not globally threatened. CITES II. Fairly common in forested blackwater regions. Occurs in several protected areas such as Imataca Forest Reserve (Venezuela) and Pedra Talhada State Park in Alagoas (Brazil).

Bibliography. Allen (1995), Bangs & Penard (1918), Berlioz (1934, 1954), Best *et al.* (1997), Bloch *et al.* (1991), Bond & Meyer de Schauensee (1943), Butler (1979), Cintra (1990), Cotton (1998a), Donahue (1994), Friedmann (1948), Grantsau (1988), Gyldenstolpe (1945b), Haverschmidt & Mees (1994), Hilty & Brown (1986), Ingels (1981), Meyer de Schauensee & Phelps (1978), Oren & Parker (1997), Parker *et al.* (1982), Remsen & T aylor (1989), do Rosário (1996), Ruschi (1949a, 1973b, 1973d, 1981-1982, 1986), Rutgers & Norris (1972), Sargeant (1994a, 1996), Scott & Brooke (1985), Sick (1993, 1997), Snyder (1966), Stotz, Fitzpatrick *et al.* (1996), Stotz, Lanyon *et al.* (1997), Terborgh *et al.* (1984), Todd (1942), Tostain *et al.* (1992), T aylor (1958a), Willard *et al.* (1991), Willis (1992), Zimmer, J.T. (1953a), Zimmer, K.J. & Hilty (1997), Zimmer, K.J. *et al.* (1997).

Genus *HELIACTIN* Boie, 1831

287. Horned Sungem

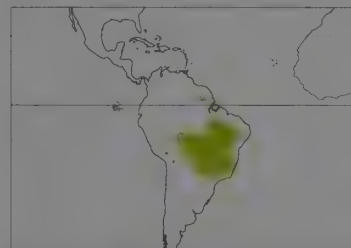
Heliactin bilopha

French: Colibri aux huppés d'or **Spanish:** Colibrí Cornudito
German: Goldhauben-Schmuckkolibri
Other common names: Sungem, Horned Hummingbird

Taxonomy. *Trochilus bilophus* Temminck, 1820, Brazil.

Species of uncertain systematic position; external morphology and behaviour indicate close affinities with *Heliothryx* and *Loddigesia*. Species name has normally been given as *H. cornuta*, but *bilopha* has priority by one year. Monotypic.

Distribution. Extreme S Surinam through CN & C Brazil (Amapá; Maranhão to Alagoas and Bahia S to São Paulo and W to W Mato Grosso, irregularly to Rondônia) to E Bolivia (Santa Cruz); also reported from Acre (extreme W Brazil).



Descriptive notes. 9.5-11 cm; 1.8-2.5 g. Male has short, straight, black bill; centre of crown shining dark blue, lateral crown tufts glittering red, blue and gold, upperparts bronzy-green; sides of head, throat and upper breast black contrasting with the white sides of neck and belly; tail feathers narrow and pointed, central four longest, central pair green, remainder white. Female lacks iridescent feathers on head and the black throat. Immature similar to female.

Habitat. Forest along rivers, woodland, cerrado, open grassland and gardens to 1000 m, most abundant below 500 m. Forages from low to middle strata.

Food and Feeding. Nectar of flowering bushes and trees like *Stachytarpheta*, *Lantana*, *Citrus*, *Malvaviscus*, Malvaceae and Urticaceae. Small insects are taken in the air by hawking.

Breeding. Jun-Oct. Near Brasília, nests have been found in May. Tiny, compact cup-shaped nest is built with soft cotton-like material and spider web, decorated outside with some lichen, on a forking branch of small bush, such as *Oureatea*, c. 1 m above the ground, occasionally higher. Clutch size 2; incubation 13 days, by female; fledging period 20-22 days. First breeding in second year.

Movements. Migratory in parts of C & E Brazil (Distrito Federal, Minas Gerais, Bahia, Espírito Santo); birds arrive in Mar and May when Verbenaceae and Labiatae flowers are in bloom. Sedentary in other areas. Migration patterns in the southern part of range are little studied. A very mobile species, as perhaps reflected by reports from far W Brazil, outside normal known range.

Status and Conservation. Not globally threatened. CITES II. Locally common. Readily accepts man-made open habitats such as gardens and cultivated areas. Has recently spread to Espírito Santo (CE Brazil), probably due to deforestation. Occurs in several protected areas throughout its range, e.g. Serra do Cipó, Brasília and Chapada dos Guimarães National Parks (Brazil) and Noel Kempff Mercado National Park (Bolivia). Until end of 1970's this hummingbird was one of the most sought after species for the international bird trade in Brazil, but this trade has now been curbed.

Bibliography. Berlioz (1964), Dubs (1992), Forrester (1993), Grantsau (1988), Haverschmidt & Mees (1994), Meyer de Schauensee (1982), Mubbs (1973a), Negret (1988), Olog (1968), Remsen & T aylor (1989), Ruschi (1967a, 1981-1982, 1982a, 1986), Sick (1993, 1997), da Silva (1997), Stotz *et al.* (1996), Willis (1992).

Genus *LODDIGESIA* Bonaparte, 1850

288. Marvellous Spatuletail

Loddigesia mirabilis

French: Loddigésie admirable **Spanish:** Colibrí Admirable
German: Violettscheitel-Flaggensylphe
Other common names: Marvellous/Peruvian Racquet-tailed Hummingbird, Loddiges's Spatuletail

Taxonomy. *Trochilus mirabilis* Bourcier, 1847, Chachapoyas, Peru.
Uncertain systematic affinities; possibly closely related to *Heliactin* and *Heliothryx*. Monotypic.
Distribution. N Peru, along E bank of R Utcubamba (Amazonas).



Descriptive notes. Male 15-17 cm (including tail 11-13 cm), female 9-10 cm (tail 5-7 cm); c. 3 g. Male has slightly decurved black bill; crest blue, hindneck brownish, postocular spot white, rest of upperparts green; gorget blue glossing blue-green, underparts white with central black line, two elongated undertail-coverts support the tail; tail very long, modified, outer feathers reduced to shafts, curved, crossing each other, terminating in two purplish-black racquets, remaining rectrices rudimentary. Female lacks crest and gorget, underparts whitish; tail elongated, lacking racquets. Immature resembles adult female, immature male with partly developed gorget, black midline on belly, and blackish racquets.

Habitat. Forest edges, second growth and montane scrub like *Rubus* thickets mixed with some *Alnus*, in open country, steep valleys and gorges at 2100-2900 m.

Food and Feeding. Nectar of flowering *Rubus*, *Bomarea formosissima* and *Staureja sericea*. Perches while feeding rather than hovering in front of flowers visited; feeds by trap-lining. Subordinate to other sympatric hummingbirds such as *Lesbia nuna*, *Colibri coruscans* and *C. thalassinus*.

Breeding. Probably Dec-Feb based on gonadal condition, although display flights have been recorded in Oct, Nov and May. No further information available.

Movements. Sedentary. Records at 1700 m and 3700 m require confirmation.

Status and Conservation. VULNERABLE. CITES II. Restricted-range species; present in North-east Peruvian Cordilleras EBA. Generally uncommon, with few recent records, and hardly any adult males have been recorded; within tiny range, an area of only c. 2000-3000 km², population seems to be small. Preferred habitat is under severe threat due mainly to destruction for firewood, together with the spread of slash-and-burn agriculture and increased incursions by grazing cattle. No protected areas exist within range; protection of some suitable patches of habitat is an urgent priority.

Bibliography. Baron (1897), Bleiweiss (1987), Boeke (1978), Bond (1954), Butler (1925), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Fjeldså (1995), Fjeldså & Krabbe (1990), Gardner (1986), Greenewalt (1966), Inskipp (1987), Parker (1976), Parker *et al.* (1982), Ruschi (1964b, 1964h, 1965a, 1965b), Rutgers & Norris (1972), Stattersfield *et al.* (1998), Stephens & Traylor (1983), Stotz *et al.* (1996), Taczanowski (1884), Taczanowski & Stolzmann (1881), Vaurie (1972), Wege & Long (1995), Zimmer (1953a).

Genus HELIOMASTER Bonaparte, 1850

289. Plain-capped Starthroat

Heliomaster constantii

French: Colibri de Constant **German:** Funkenkehlkolibri **Spanish:** Colibrí Pochotero
Other common names: Constant's Starthroat

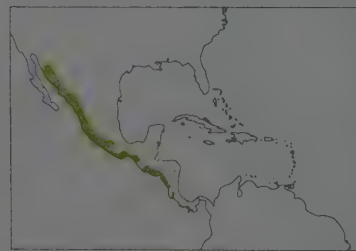
Taxonomy. *Ornismya Constantii* DeLatre, 1843, Guatemala; error = Bolsón, Costa Rica.
Present species and *H. longirostris* occasionally separated in genus *Anthosenus*, on basis of squarish tail, rounded rectrices and details of bill morphology; however, the distinguishing features vary in a continuum between these species and *H. furcifer*, with *H. squamosus* occupying intermediate position, and treatment of all four as congeners now generally accepted; some authors also merge *Rhodopis*. Intergradation between race *leocadiae* and nominate apparently occurs in El Salvador. Proposed race *sardus* of W Mexico now usually considered a synonym of *leocadiae*. Three subspecies recognized.

Subspecies and Distribution.

H. c. pinicola (Gould, 1853) - NW Mexico (S to Jalisco).

H. c. leocadiae (Bourcier & Mulsant, 1852) - W & SW Mexico and W Guatemala.

H. c. constantii (DeLatre, 1843) - El Salvador to S Costa Rica.



Descriptive notes. 11.5-12.5 cm; male 8-1 g, female 7-2 g. Male has straight black bill; upperparts dark bronzy-green, dusky on the crown, with distinctive white stripe down centre of rump; tail greenish-bronze, the distal third black, outer three rectrices tipped white; bold white postocular and malar stripes; chin and face greyish, gorget mostly red; underparts mostly dull grey, flecked with green on sides; centre of belly and tuft on each side of rump white. Female often has upper half or more of gorget greyish; broader white tips to outer three rectrices. Immature has entire gorget greyish, broad buffy-white fringes on head, gorget,

chest, sides, back and rump; white stripe on lower back tinged buffy. Race *pinicola* much paler below, chin sooty-grey, red of gorget less extensive; *leocadiae* has gorget pinker, and is generally similar to previous race but underparts darker, though still paler than in nominate.

Habitat. Canopy and edge of dry deciduous forest, borders of evergreen gallery forest, dry scrub, isolated savanna trees, coffee plantations, etc.; usually flies and perches well above ground. Ranges in altitude from sea-level to 1500 m in Mexico, 1200 m in Honduras, and to 1000 m in Costa Rica. Mainly on Pacific slope, reaching Caribbean slope locally in dry, rain-shadow interior valleys.

Food and Feeding. Nectar of various trees (*Erythrina*, *Cieba*, *Tubebuia*, *Bombacopsis*, *Genipa*), large cacti (*Opuntia*, *Nopalea*), shrubs (*Hamelia*, *Manihot*), vines (*Bignoniaceae*, *Convolvulaceae*, *Mandevilla*), and sometimes from *Heliconia* in gallery forest or *Bromelia* in understorey and edges of dry forest. Often aggressive, defending territories in flowering trees (sometimes whole trees) or invading territories of smaller species. Frequently flycatches during prolonged bouts of hovering and darting high above ground; less often gleans arthropods from foliage and branches of trees.

Breeding. Late wet and early dry seasons, Oct-Jan or Feb (El Salvador, Costa Rica); Mar (perhaps) to Jun in NW Mexico. Nest a shallow cup of pale-coloured plant down and spider web, decorated with bits of bark and lichen, usually in exposed position well up in tree at forest edge or isolated tree in savanna. No further information.

Movements. Apparently migratory at N end of range, disappearing between Oct-Nov and Feb; in other areas pronounced local seasonal movements following shifts in flowering.

Status and Conservation. Not globally threatened. CITES II. Uncommon to locally common; several protected areas are to be found in its range, such as Guanacaste, Santa Rosa and Palo Verde National Parks in Costa Rica; seems able to tolerate much disturbance, as long as at least scattered trees remain.

Bibliography. Anon. (1998a), Arizmendi (1987), Arizmendi & Ornelas (1990), Binford (1989), Des Granges (1979), Des Granges & Grant (1980), Dickey & van Rossem (1938), Feinsinger (1976, 1980), Fogden (1993), Friedmann *et al.* (1950), Griscom (1932a), Howell & Webb (1995a), Johnsgard (1997), Kaufman (1996), Land (1970), Monroe (1968), Ridgway (1911), van Rossem (1945a), Rowley (1966), Schaldach (1963), Slud (1964, 1980), Stiles (1985c), Stiles & Skutch (1989), Stone (1932), Stotz *et al.* (1996), Thurber *et al.* (1987), Wagner (1957b), Wetmore (1941), Witzeman (1979), Wolf (1970).

290. Long-billed Starthroat

Heliomaster longirostris

French: Colibri corinne **German:** Rosenkehlkolibri **Spanish:** Colibrí Piquilargo

Taxonomy. *Trochilus longirostris* Audebert and Vieillot, 1801, Trinidad.

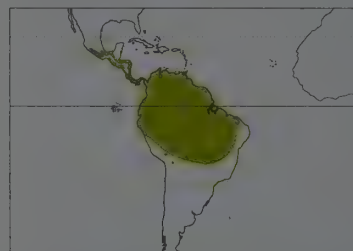
Present species and *H. constantii* occasionally separated in genus *Anthosenus*, on basis of squarish tail, rounded rectrices and details of bill morphology; however, the distinguishing features vary in a continuum between these species and *H. furcifer*, with *H. squamosus* occupying an intermediate position, and treatment of all four as congeners now generally considered more appropriate; some authors also merge *Rhodopis*. Several additional races described, notably *masculinus* (SC Mexico), *veraguensis* (Panama), *chalcurus* (Costa Rica), *stuartae* (Colombia) and *caeruleitres* (Bolivia), but most have not been sustained and now included within nominate; separation of *pallidiceps* from nominate has been questioned. Three subspecies currently recognized.

Subspecies and Distribution.

H. l. pallidiceps Gould, 1861 - S Mexico to Nicaragua.

H. l. longirostris (Audebert & Vieillot, 1801) - E & SW Costa Rica, Panama and Colombia S to E Bolivia and C & NE Brazil; Trinidad.

H. l. albicrissa Gould, 1871 - W Ecuador and NW Peru.



Descriptive notes. 11-12 cm; male 7-1 g, female 6-5 g. Male has long, straight, black bill; crown glittering blue to greenish-blue, rest of upperparts rather dark bronzy-green, with a white stripe down centre of rump; tail short, square-tipped, black distally, outer 2-3 rectrices tipped white; small postocular spot and broad malar stripe white, chin blackish, gorget dark metallic purple; breast grey, sides bronze-green, centre of lower breast and belly dull white, tufts on each side of rump white; undertail-coverts grey, edged with white. Female often shows some blue on crown, but never as much as male; gorget narrower, largely dusky grey. Immature

of both sexes with gorget dusky blackish, sometimes glossed with purple; no blue on crown; feathers of gorget, head, breast, sides and back with broad buffy fringes, those of lower back and rump with more cinnamon-buff fringes. Race *pallidiceps* has crown more greenish-blue, sides of breast more extensively golden-bronze; *albicrissa* has undertail-coverts mostly or entirely white.

Habitat. In more humid areas than *H. constantii*; prefers forest canopy, especially at breaks or along edges, open woodland, isolated groves and trees in pastures and clearings, gallery woodland in open country, second growth and semi-open vegetation; avoids shady interior of forest. Lowlands and foothills, locally to 1400-1500 m.

Food and Feeding. Takes nectar from flowers of a variety of mostly large trees, being especially fond of those of *Erythrina* species with long, narrow corollas; also flowers of climbing vines, shrubs, *Heliconia* and cultivated banana, feeding lower along edges and in second growth. Traps small flowering trees, often over wide areas, and may defend trees with many flowers. Often hovers high in the air, darting repeatedly at flies and gnats; gleans from foliage at least occasionally, arthropod food including spiders as well as many flies (Diptera) and Hymenoptera.

Breeding. Late wet to early dry seasons, Oct-Nov through Feb-Mar in S Mexico and Central America; Mar and Sept-Oct in N Colombia; no information for other areas. Nest a broad, shallow cup of sprigs of moss and liverworts, plant down and spider web decorated with bits of grey lichen, placed in shrub or on exposed horizontal branch of (often dead) tree, mostly 4-5-12 m above ground, sometimes on telephone wire. Clutch size 2; incubation 18.5-19 days; fledging period 25-26 days; chick dark with upperparts, throat and breast covered with short tufts of whitish down at c. 2 weeks, more abundant than on most hummingbird nestlings; following fledging, young fed by parent for up to 22-23 days more. Second broods very rarely recorded Mar/Apr in Central America.

Movements. Poorly understood; in most areas presence seems to be erratic, the species disappearing for some seasons; in Costa Rica, appears when *Erythrina* blooms in dry season between late Nov and early Feb when disappears again.

Status and Conservation. Not globally threatened. CITES II. Uncommon in most areas, but evidently able to tolerate much disturbance, and perhaps even favoured by deforestation, as long as scattered trees and groves remain. Occurs in several protected areas, e.g. Carara Biological Reserve, Corcovado National Park and Gofito National Wildlife Refuge (Costa Rica), Asa Wright Nature Centre (Trinidad), Tayrona National Park (Colombia) and Brasília National Park (Brazil).
Bibliography. Berg (1994), Best & Clarke (1991), Best *et al.* (1997), Binford (1989), Bloch *et al.* (1991), Bond & Meyer de Schauensee (1943), Costa & Bornschein (1995), Dickey & van Rossem (1938), Fjeldså & Krabbe (1990), Friedmann *et al.* (1950), Grantsau (1988), Griscom (1932a), Gyldestolpe (1945b), Haverschmidt & Nies (1994), Herklots (1961), Hilty & Brown (1986), Howell & Webb (1995a), Johnsgard (1997), Lowery & Dalquest (1951), Meyer de Schauensee & Phelps (1978), Monroe (1968), Navarro (1986), Navarro, Peterson & Escalante (1992), de la Peña (1994), Phelps & Phelps (1958), Phillips (1966), Pople *et al.* (1997), Ridgely & Gwynne (1989), Ridgway (1911), Rowley (1966), Ruschi (1981-1982, 1986), Rutgers & Norris (1972), Salaman & Mazariegos (1998b), Schmitt & Schmitt (1987), Sick (1993, 1997), Skutch (1972), Slud (1964), Snyder (1966), Stiles (1980), Stiles & Skutch (1989), Stotz *et al.* (1996), Thurber *et al.* (1987), Todd & Carricker (1922), Tostain *et al.* (1992), Wagner (1946a), Wetmore (1941, 1968a), Williams & Tobias (1994), Willis & Eisenmann (1979), Willis & Oniki (1993), Zimmer (1953a).

291. Stripe-breasted Starthroat

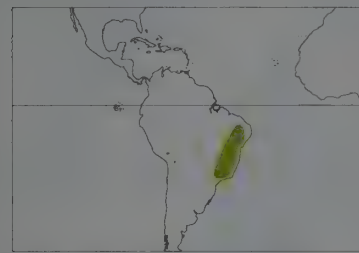
Heliomaster squamosus

French: Colibri médiastin **German:** Violettkehlkolibri **Spanish:** Colibrí Escamoso
Other common names: White-striped Hummingbird

Taxonomy. *Trochilus squamosus* Temminck, 1823, Bahia, Brazil.

Present species has occasionally been separated in genus *Lepidolarynx*; however, details of tail and bill morphology vary in a continuum from *H. constantii* and *H. longirostris* to *H. furcifer*, with present species occupying an intermediate position, and treatment of all four as congeners now generally considered more appropriate; some authors also merge *Rhodopis*. Monotypic.

Distribution. E Brazil (Pernambuco through Bahia, Goiás and Minas Gerais to São Paulo).



Descriptive notes. 11-12 cm; 5-6.5 g. Male has long, decurved black bill; crown iridescent green, upperparts bronze-green; throat glittering violet, lateral feathers lengthened; underparts greenish-black with white central band; tail forked, central feathers as back, rest dark blue-green. In Jul, after breeding, male adopts eclipse plumage, with greyish throat, spotted blackish; regains breeding plumage in Oct. Female above similar; throat feathers blackish-green edged white, below greyish with white central stripe, greenish on flanks; tail slightly forked, green, outer rectrices with steel blue subterminal band, tipped white. Immature similar to female.

Habitat. Forest, savanna, from lowlands to 800 m.

Food and Feeding. Nectar of flowering native and introduced shrubs and trees, such as *Hibiscus*, *Erythrina*, *Spathodea*, *Tabebuia*, *Delonix*, *Costus*, *Heliconia*, *Vochysia*, *Bilbergia* and *Eucalyptus*; forages 3-8 m above ground. Insects are caught in the air by hawking.

Breeding. Feb-Apr. Small cup-shaped nest is built on horizontal tree branches, 6-8 m above ground, occasionally higher. Clutch size 2; incubation 14-16 days, by female; chick is black with greyish dorsal down; fledging period 21-24 days. First breeding in second year.

Movements. Sedentary.

Status and Conservation. Not globally threatened, CITES II. Locally common, for example in Serra da Mantiqueira. Occurs in Serra da Canastra National Park (Minas Gerais). Until end of 1970's, was commonly exported from Brazil, but this trade is now at an end.

Bibliography. dos Anjos *et al.* (1997), Elgar (1976), Forrester (1993), Grantsau (1988), Oniki (1996), Ruschi (1953b, 1962d, 1964a, 1981-1982, 1986), Sargeant (1996), Sick (1993, 1997), Silveira (1998), Stotz *et al.* (1996), Willis (1992).

292. Blue-tufted Starthroat

Heliomaster furcifer

French: Colibri d'Angèle

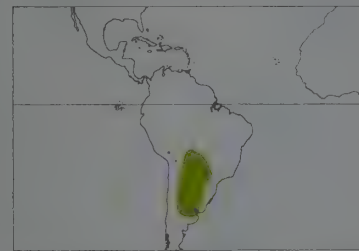
German: Blaubartkolibri

Spanish: Colibrí de Barbijo

Taxonomy. *Trochilus furcifer* Shaw, 1812, Paraguay.

Formerly isolated as the only species in present genus, on basis of forked tail, pointed rectrices and details of bill morphology, the remaining three species being placed in genera *Anthoscenus* and *Lepidolarynx*; however, the distinguishing features vary in a continuum between present species and *H. constantii* and *H. longirostris*, with *H. squamosus* occupying an intermediate position, and treatment of all four as congeners now generally accepted; some authors also merge *Rhodopis*. Monotypic.

Distribution. C & E Bolivia (from Cochabamba and Tarija), Paraguay and C & S Brazil (Mato Grosso and Goiás to Rio Grande do Sul) S to Uruguay and N Argentina (S to Catamarca, Córdoba and N Buenos Aires). Single records from SE Colombia (Leticia) and NE Ecuador (E Napo).



Descriptive notes. 12-6-13 cm; 5-6.5 g. Male has long, slightly decurved black bill; crown, nape and upper mantle emerald green, rest of upperparts shining coppery green; throat glittering violet, sides of neck (with elongated lateral feathers) and underparts iridescent ultramarine; tail forked, pointed, dark green above, blue-green below. In Jul, after breeding, male adopts eclipse plumage, greyish below like female; regains breeding plumage in Oct. Female coppery green above, throat grey, mottled darkish with increasing age, underparts grey with white line down centre of belly, green discs on sides; tail slightly forked, pointed, bronze-green above, central tail

feathers black distally, shining blue-green below, outer feathers tipped white. Immature similar to female.

Habitat. Forest border, *cerrado* and lowland grasslands.

Food and Feeding. Nectar of flowering Lanthaceae, Leguminosae, Zingiberaceae, Bromeliaceae, Liliaceae, Lobeliaceae, Verbenaceae and Cactaceae; foraging at heights of 2-8 m. Hawks for insects in the air. Male defends nectar-rich territories.

Breeding. Nov-Mar. Cup-shaped nest of soft seed fibre, outside decorated with lichen, is built 3-6 m above the ground. Clutch size 2; incubation 15-16 days, by female; chick is black with some greyish dorsal down; fledging at 20-25 days. First breeding in second year.

Movements. Poorly known. Apparently performs some sort of migration or at least dispersal; reports of birds well outside normal known range, in Colombia and Ecuador, probably refer to migrants.

Status and Conservation. Not globally threatened, CITES II. Locally fairly common to rare. Present in Chancani Park and Nature Reserve. Commonly exported in the bird trade from Brazil until the end of 1970, but this activity has now been terminated.

Bibliography. Belton (1984), Bond & Meyer de Schauensee (1943), Canevari *et al.* (1991), Cintra & Yamashita (1990), Contreras *et al.* (1990), Dubs (1992), Forrester (1993), Grantsau (1988), Hill (1992), Hilty & Brown (1986), Klimatis & Moschione (1987), Laubmann (1930), Lowen, Bartrina, Clay & Tobias (1996), Nores *et al.* (1983), de la Peña (1994), Remsen & Traylor (1989), do Rosário (1996), Ruschi (1962d, 1964a, 1973b, 1973d, 1981-1982, 1986), Rutgers & Norris (1972), Short (1975), Sick (1993, 1997), Stotz *et al.* (1996), Wetmore (1926).

Genus RHODOPIS Reichenbach, 1854

293. Oasis Hummingbird

Rhodopis vesper

French: Colibri vesper

German: Atacamakolibri

Spanish: Colibrí del Atacama

Taxonomy. *Ornismya vesper* Lesson, 1829, probably near Tarapacá, Chile (but possibly western Peru).

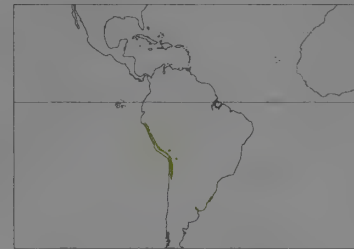
Closely related to *Heliomaster*, and sometimes included within that somewhat varied genus. Intraspecific variation very slight, and in need of revision; proposed race *tertia* (N Peru) tentatively included in nominate, although morphometrically inseparable from *atacamensis*; species may be better considered monotypic. Three subspecies tentatively recognized.

Subspecies and Distribution.

R. v. knoepekeae Berlioz, 1974 - NW Peru (Cerro Illescas in SW Piura).

R. v. vesper (Lesson, 1829) - most of Peru and extreme N Chile (Tarapacá).

R. v. atacamensis (Leybold, 1869) - N Chile (Atacama).



Descriptive notes. 13-13.5 cm; 3-6-4.2 g. Male has medium-sized curved bill, black; upperparts shining olive green, rufous on rump and uppertail-coverts; throat iridescent rosy violet with turquoise lateral patches, underparts buffy white; tail deeply forked, central rectrices greyish-olive, outer four much narrower than others, deep purplish-brown. In eclipse plumage, male has dull brown throat. Female above similar to male; below buffy white; tail slightly forked, shining olive, outer rectrices black on terminal quarter, tipped white. Immature similar to adult female. Races all very similar: *atacamensis* like nominate but smaller, with bill

shorter and more slender; *knoepekeae* like previous race but smaller, bill shorter and more slender, rufous of rump and uppertail-coverts less developed.

Habitat. Arid steppes, oases, gardens, lowlands and mountains up to 3000 m. Most abundant on coastal hills below 800 m.

Food and Feeding. Nectar of flowering shrubs, cacti and trees, Malvaceae and Leguminosaceae in particular. Aerial insects are caught by hawking, other small arthropods gleaned from leaves.

Breeding. Sept-Nov; small cup-shaped nest is suspended from overhanging branches, often in fig, lemon and orange trees, 3-5 m above the ground, sometimes higher. Clutch size 2; incubation 15-16 days, by female; fledging period 22-24 days. First breeding in second year.

Movements. Mostly sedentary; local altitudinal movements have been reported for *atacamensis*.

Status and Conservation. Not globally threatened, CITES II. Common in all arid zones. Readily occupies man-made habitats. Occurs in Paracas National Park (Peru). Trapping rate for wild bird trade was significant in Peru until 1990, but this seems to have declined.

Bibliography. Araya & Chester (1993), Cook (1996), Fjeldsá & Krabbe (1990), González & Málaga (1997), Hesse & Hesse (1986), Johnson (1967, 1972), Koepeke (1970), Meyer de Schauensee (1982), Nadal *et al.* (1987), Parker *et al.* (1982), Stotz *et al.* (1996), Zimmer (1930, 1953a).

Genus THAUMASTURA Bonaparte, 1850

294. Peruvian Sheartail

Thaumastura cora

French: Colibri cora

German: Corakolibri

Spanish: Colibrí Cora

Other common names: Cora's Sheartail

Taxonomy. *Orthorhynchus Cora* Lesson and Garnot, 1827, between Callao and Lima, western Peru. Affinities of genus uncertain; external morphology indicates close relationship with *Doricha*, *Tilmatura*, *Microstilbon* and *Rhodopis*; genus sometimes merged into *Calliphlox*. Monotypic.

Distribution. W Peru (Piura and Lambayeque to Tacna) and N Chile (Arica). Single report from SW Ecuador (Loja).



Descriptive notes. Male 13 cm (tail 7 cm), female 7-8 cm; 2-2.5 g. Male has short, straight, black bill; upperparts iridescent green; throat shining rosy purple to turquoise on lateral parts of gorget, breast white, rest of underparts greyish with green discs; central tail feathers very short and mainly white, next pair extremely long and brittle, mostly white with dark brown tips and dark shafts, remaining feathers dark brown with white inner webs and tips, steadily decreasing in length towards outermost pair. After breeding season, male adopts eclipse plumage, glittering gorget becomes dull whitish with small central brown spots, and tail

streamers moulted. Female above like male; below pale cinnamon and white; lacks elongated tail, inner feathers shining green, rest black, tipped white, outer rectrices shortest. Immature similar to adult female.

Habitat. Inhabits semi-arid coastal zone and lower slopes of Andes up to 2400 m; most numerous at sea-level.

Food and Feeding. Nectar of flowering shrubs, cacti and trees such as *Russelia*, *Melocactus*, *Cordia* and Malvaceae at heights of 2-5 m. Insects are caught in the air by hawking, and occasionally collected from the surface of leaves. Male defends territories in flowering shrubs and trees.

Breeding. Jun-Oct; small cup-shaped nest of fine plant fibre and spider web is built in fork of vertical branches, 3-6 m above the ground; clutch size 2; incubation 15-16 days, by female; chick black with sparse greyish dorsal down; fledging at 20-23 days. First breeding in second year.

Movements. Mostly sedentary; altitudinal movements of individuals reported at end of breeding season. Single report from Ecuador might refer to a migrant.

Status and Conservation. Not globally threatened, CITES II. Common resident in the semi-arid coastal ranges, with densities of at least 3-5 pairs/km². Readily accepts man-made habitats like gardens and farmland. As a recent arrival to Chile, the species locally dominates *Myiis yarellii*, with a potentially adverse effect on the population of the latter.

Bibliography. Araya & Chester (1993), Fjeldsá & Krabbe (1990), González & Málaga (1997), Howell & Webb (1995b), Johnson (1967, 1972), Koepeke (1970), Meyer de Schauensee (1982), Olrog (1968), Parker *et al.* (1982), Stotz *et al.* (1996), Zimmer (1930, 1953a).



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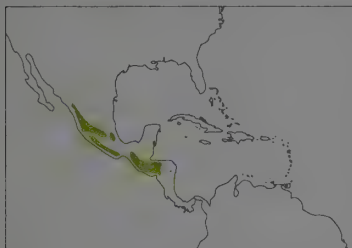
Genus *TILMATURA* Reichenbach, 1855

295. Sparkling-tailed Woodstar

Tilmatura dupontii

French: Colibri zémès **German:** Blaukehl-Sternkolibri **Spanish:** Colibrí de Dupont
Other common names: Sparkling-tailed/Dupont's Hummingbird

Taxonomy. *Ornismya dupontii* Lesson, 1832, Mexico. Systematic position uncertain; probably closely related to *Calliphlox*, and sometimes merged into an expanded version of this genus; alternatively placed in *Philodice*. Monotypic.
Distribution. C & S Mexico (C Sinaloa, México and Veracruz to Chiapas) through highlands of Guatemala, El Salvador and Honduras to N Nicaragua.



Descriptive notes. Male 9-10 cm (including tail of c. 3 cm), 2.4-3.3 g; female 6.5-7.5 cm, 2.4-2.8 g (one 4-1 g). Male has straight black bill; upperparts metallic bronzy-green, postocular spot white; iridescent violet-blue gorget, whitish band across breast, lower underparts dusky green, white patch on either side of rump; tail long, deeply forked, barred black and white with some rufous. Female has straight black bill; short black eyestripe, upperparts bronzy-green, postocular spot white; underparts cinnamon with white patches on both sides of rump; tail forked, double-lobed, central pair of rectrices shining green with black subterminal

spots, outer rectrices purple-black with white subterminal band tipped pale cinnamon. Immature resembles adult female; immature male has green mottling on underparts, throat with blue discs, outer rectrices tipped white.

Habitat. Edges of humid to semi-arid forest, open woodland with oak trees, second growth, at 500-2500 m; seasonally in subtropical evergreen forest (Honduras) near sea-level.

Food and Feeding. Trap-lines for nectar of a great variety of flowers; hawks for insects in the air during extended flights.

Breeding. Birds in breeding condition reported for Aug; no further information available.

Movements. Seasonal altitudinal movements most likely following breeding season.

Status and Conservation. Not globally threatened. CITES II. Uncommon to fairly common. No immediate threat recorded, and evidence suggests that species may accept man-made habitats to some extent; distributional range contains several protected areas including national parks. Regularly recorded in Sierra de Atoyac (Guerrero) and Lagos de Montebello (S Chiapas).

Bibliography. Anon. (1998a), Berlitz (1938), Binford (1989), Brown & Bowers (1985), Davis (1953), Des Granges & Grant (1980), Edwards & Lea (1955), Friedmann *et al.* (1950), Griscom (1932c, 1934), Howell & Webb (1992a, 1995a), Johnsgard (1997), Land (1970), Marshall (1943), Monroe (1968), Ridgway (1911), Rosenberg & Rosenberg (1979), Stoltz *et al.* (1996), Thurber *et al.* (1987), del Toro (1941), Wagner (1946a, 1957b), Wetmore (1941).

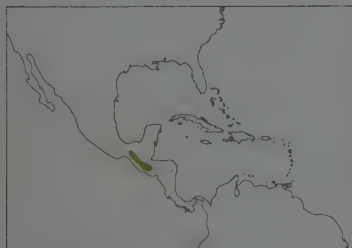
Genus *DORICHA* Reichenbach, 1854

296. Slender Sheartail

Doricha enicura

French: Colibri à queue singulière **Spanish:** Colibrí Coliraro
German: Scherenschwanz-Sternkolibri

Taxonomy. *Trochilus enicura* Vieillot, 1818, Brazil; error = Guatemala. Genus sometimes merged into *Calothorax*, or an expanded version of *Calliphlox*. Monotypic.
Distribution. Mountains and interior valleys of S Mexico (Chiapas) to Guatemala, Honduras and El Salvador.



Descriptive notes. Male 11-12.5 cm (including long tail), 2-3 g; female 8-9 cm, 2-6 g. Male has long, decurved black bill; head and upperparts green; white postocular spot; blackish chin, gorget pinkish-purple, white band on lower breast, belly green with whitish centre; very long tail deeply forked, central rectrices green, remaining ones blackish. Female has upperparts green, with white postocular spot; underparts cinnamon-buff, blackish auricular stripe; tail shorter than in male, less forked, central rectrices green, outer rectrices cinnamon with broad blackish band and white tips. Immature similar to female.

Habitat. Openings in forest, woodland, second growth and scrub, at 1000-3000 m.

Food and Feeding. Forages mainly in low to middle strata, often near ground. Feeds on a combination of nectar and small arthropods.

Breeding. Recorded breeding in Oct in Chiapas. Nest and eggs apparently unknown.

Movements. Sedentary, though seasonal fluctuations in abundance.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in North Central American Highlands EBA. Status throughout range poorly known; species generally

reckoned to vary from rare to locally common. Main threat is rapid conversion of preferred habitat to agriculture, in combination with the restricted and local distribution.

Bibliography. Anon. (1998a), Dickey & van Rossem (1938), Friedmann *et al.* (1950), Griscom (1932a), Hernández-Baños *et al.* (1995), Howell & Webb (1995a), Johnsgard (1997), Land (1970), Monroe (1968), Moore (1939b), Rand & Traylor (1954), Stattersfield *et al.* (1998), Stoltz *et al.* (1996), Thurber *et al.* (1987), Wetmore (1941).

297. Mexican Sheartail

Doricha eliza

French: Colibri élise **German:** Rosenkehl-Sternkolibri **Spanish:** Colibrí de Elisa

Taxonomy. *Trochilus eliza* Lesson and DeLattre, 1839, between Veracruz and Jalapa, Veracruz, Mexico.

Genus sometimes merged into *Calothorax*, or an expanded version of *Calliphlox*. The two populations of present species show some differences in plumage characters, possibly representing two races. Monotypic.

Distribution. SE Mexico, in C Veracruz and N coast of Yucatán Peninsula (E to Holbox I).



Descriptive notes. Male 9.5-10 cm (including moderately long tail), female 8.5-9 cm; 2.4-2.6 g. Male has long, moderately decurved black bill; upperparts green; gorget rosy purple, with white band across upper breast; lower breast and belly whitish, laterally washed green, undertail-coverts washed cinnamon; tail long and forked, central rectrices green, rest blackish with inner webs cinnamon. Female has upperparts similar to male; underparts whitish with sides and flanks washed buffy cinnamon; tail shorter than in male. Immature resembles female; seems to exhibit some form of delayed plumage maturation, as most individuals noted

in Feb and Mar in Yucatán were in a female-like plumage.

Habitat. Mangrove edge, arid scrub and parklands. Yucatán population found principally in arid scrub.

Food and Feeding. Observed feeding, presumably on nectar, at terrestrial *Ipomoea* and *Justicia*; also at *Helicteres guazumaefolia*. Diet is supplemented by small arthropods.

Breeding. Breeding condition in May, and nest with small chicks in early Aug, in Veracruz; nesting in Aug-Apr, in Yucatán, with recently fledged young reported in Feb and Mar. Nest usually low, e.g. at 1-3 m in fork of *Calea urtisifolia* bush, but sometimes in top of palm tree; cup-shaped nest, made of seeds of Compositae, lichens and spiders' webs. Clutch size 2; one nest found containing 3 chicks, presumably as a result of dump-laying by another female; chicks fed by female for some time after leaving nest, but period not documented.

Movements. Only movements noted were apparently local.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Yucatán Peninsula Coastal Scrub EBA. Veracruz population endangered on the basis of extremely restricted distribution and very localized population structure. Yucatán population, in spite of its extremely limited range, is probably not threatened, unless widespread development of the region for tourism were to extend across the zone.

Bibliography. Anon. (1998a), Friedmann *et al.* (1950), Hernández-Baños *et al.* (1995), Howell & Webb (1995a), Johnsgard (1997), Ortiz-Pulido *et al.* (1998), Paynter (1955), Ridgway (1911), Stattersfield *et al.* (1998), Stoltz *et al.* (1996).

Genus *CALLIPHLOX* Boie, 1831

298. Bahama Woodstar

Calliphlox evelynae

French: Colibri des Bahamas **German:** Bahamasternkolibri **Spanish:** Colibrí de las Bahamas

Taxonomy. *Trochilus Evelynae* Bourcier, 1847, Nassau, New Providence Island, Bahamas. Sometimes separated, along with *C. bryantae* and *C. mitchellii*, in genus *Philodice*; in older works separated in *Nesophlox*, alone or occasionally with *C. bryantae*. Proposed race *salina*, from Caicos Is, not separable in from nominate. Two subspecies recognized.

Subspecies and Distribution.

C. e. evelynae (Bourcier, 1847) - Bahamas (except Inagua).

C. e. lyrura (Gould, 1869) - Inagua.



Descriptive notes. 7.8-8.2 cm; 2.5-3.3 g. Male has short, slightly decurved black bill; back iridescent green; small postocular white spot, chin and throat glittering violet-purple, breast whitish, belly rufous with green admixed, lower flanks rufous; tail deeply forked, central tail feathers green, others with partly cinnamon-rufous inner webs. After breeding, iridescent throat of male is replaced by pale grey eclipse plumage. Female upperparts dull green; small whitish postocular spot, chin and throat pale grey with small green discs, chest whitish, belly rufous; tail rounded, central tail feathers green, others cinnamon with broad black subterminal band. Immature similar to adult female. Male of race *lyrura* has metallic reddish-purple forehead.

Habitat. Occurs in all island habitats: coastal range to pine forests, gardens and parks.

Food and Feeding. Nectar of flowering shrubs, vines and trees (native and introduced), including *Russelia*, *Leonotis*, *Ipomea*, *Euphorbia fulgens*, *Pedilanthus*, *Duranta*, *Lantana*, *Stachytarpheta*, *Ernodes*, *Dicliptera*, *Cordia* and *Bauhinia*. Insects are caught in the air by hawking. Males defend territories in flowering shrubs and trees.

Breeding. Nests all year round; main nesting season Jan-Apr and in May on southern island Inagua. Tiny cup-shaped nest of fine plant fibre and spider web, lined with soft cotton-like material, outside decorated with small pieces of bark, is built in fork of small branches, 3-7 m above the ground. Nests of race *lyrura* are built much lower down, at 1-3 m. Clutch size 2; incubation 15-16 days, by female; chick black with grey dorsal down; fledging period 20-24 days. Young remain with parent bird for another 20-30 days. First breeding in second year.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Bahamas EBA. Common resident throughout range, with densities of at least 12-15 pairs/km². Race *lyrura* of Inagua abundant only along coastal areas with towns, rare inland.

Bibliography. Anon. (1998a), Bond (1985), Brudenell-Bruce (1975), Buden (1987a, 1987b, 1993), Emlen (1977), Fisk (1974), Greenway (1936), Johnsgard (1997), Langridge & Sykes (1974), Miller (1978), Northrop (1891), Owre (1976), Paterson (1972a), Raffaele *et al.* (1998), Ridgway (1911), Schuchmann (1989), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Terres (1982), Todd (1942), Tyrrell & Tyrrell (1990), White (1998).

299. Magenta-throated Woodstar

Calliphlox bryantae

French: Colibri magenta **German:** Violettkehl-Sternkolibri **Spanish:** Colibri Magenta

Taxonomy. *Doricha bryantae* Lawrence, 1867, Costa Rica.

Often separated with *C. mitchellii*, and sometimes *C. evelynae*, in genus *Philodice*; in past, occasionally placed with *C. evelynae* in *Nesophlox*. Monotypic.

Distribution. N Costa Rica to W Panama, mainly on Pacific slope.



Descriptive notes. Male 9 cm, 3-3 g; female 7-5 cm, 3-5 g. Male has short, straight, black bill; upperparts bronzy-green, short central rectrices tipped black, progressively longer lateral rectrices black with cinnamon-rufous inner webs; postocular spot white, gorget metallic purple, set off by conspicuous white collar across foreneck; breast and sides green, belly rufous; white or buffy patch on each side of rump. Female has upperparts like male, auriculars greyish, throat buffy, white collar less distinct, green of breast and sides mixed with rufous; tail double-rounded, lateral rectrices rufous with black subterminal band

and buffy cinnamon tip. Immature resembles adult female but paler below and shows buffy fringes on the head and nape, and with smaller (male) or larger (female) pale tips to the outer rectrices.

Habitat. Forest borders and clearings, thinned woodland, second growth, scrubby pastures, semi-open mountain slopes, at 700-1850 m (Costa Rica), 1100-1750 m (Panama).

Food and Feeding. Takes nectar from flowers of low trees (*Inga*, *Quararibea*), shrubs (*Lantana*) and herbs (*Lobelia*); where flowers are abundant many often gather in quarrelsome aggregations with much chasing and supplanting, both sexes sometimes defending feeding territories; territorial male gives dive displays. Long, deeply forked tail of male usually held cocked and closed while feeding, opened widely during aggressive displays. Arthropods taken by hawking from perch or gleaning in lower foliage.

Breeding. Nov-Mar or Apr (Costa Rica). Breeding male gives dive displays also in small groups, probably leks, around forest clearings away from flowers. Nest undescribed.

Movements. Evidently makes at least local movements, since at a given locality can be common to abundant at one time of year and absent at others, but more information required.

Status and Conservation. Not globally threatened. CITES II. Currently considered Near-threatened. Restricted-range species: present in Costa Rica and Panama Highlands EBA. Locally common, at least seasonally, throughout much of range but movements poorly understood; seems able to tolerate, and perhaps benefit from, at least partial forest clearance. Occurs in Monteverde Biological Reserve (Costa Rica).

Bibliography. Anon. (1998a), Carriger (1910), Feinsinger (1976, 1977, 1980), Fogden (1993), Ridgely & Gwynne (1989), Slud (1964), Stattersfield *et al.* (1998), Stiles (1985c), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968a).

300. Purple-throated Woodstar

Calliphlox mitchellii

French: Colibri de Mitchell **German:** Purpurkehl-Sternkolibri **Spanish:** Colibrí de Mitchell
Other common names: Mitchell's Woodstar

Taxonomy. *Trochilus Mitchellii* Bourcier, 1847, Zimapan, Ecuador.

Often separated in genus *Philodice*, alone, or with *C. bryantae*, sometimes also *C. evelynae*, and less commonly *Tilmatura dupontii*. Birds from Panama were initially misidentified as *Chaetocercus heliodor*. Monotypic.

Distribution. E Panama (Darién) through W Colombia (both slopes of the W Andes) to W Ecuador (S to El Oro and Loja).



Descriptive notes. 6-8-7-5 cm; 3-0-3-3 g. Male has short, straight, black bill; upperparts dusky bronzy-green, with white patch on either side of rump; throat and sides of neck shining violet-purple, breast white, belly dusky bronze, flanks and belly rufous; tail forked, brownish-purple, central tail feathers shortish, outer two pairs longest, outermost pair narrow. Female has upperparts similar to male; white line behind eye, throat buffy white speckled dusky at sides, whitish band across upper breast, green band below, belly rufous; central tail feathers same colour as back, rest cinnamon with black subterminal band. Immature similar to adult female.

Habitat. Humid forest, forest borders from coast to cloudforest at 2400 m (Nariño, Colombia); in SW Colombia, Dec-May, most numerous above 1000 m. Mainly forages in tree tops.

Food and Feeding. Nectar of flowering trees, such as *Cordia* and *Inga*. Small insects are caught in the air by hawking. Male defends territories in flowering trees.

Breeding. Dec-May in SW Colombia. Tiny cup-shaped nest of fine fibre and spider web is placed on thick branches in tall trees, often 8-12 m above the ground. Clutch size 2; incubation 15-17 days, by female. No further information.

Movements. Altitudinal movements during breeding period in SW Colombia. Birds at higher elevations are engaged in breeding.

Status and Conservation. Not globally threatened. CITES II. Uncommon to locally common. Seems to depend on native flowering trees, especially *Inga*, as major source of nectar. Occurs in La Planada Reserve (Colombia).

Bibliography. Anon. (1998a), Best *et al.* (1997), Butler (1979), Fjeldså & Krabbe (1990), Hilty (1997), Hilty & Brown (1986), Kirwan & Marlow (1996), Miller (1963), Ridgely & Gwynne (1989), Robbins *et al.* (1985), Ruschi (1962e, 1964c, 1981-1982), Salaman & Mazariegos (1998b), Stotz *et al.* (1996), Wetmore (1968a), Williams & Tobias (1994).

301. Amethyst Woodstar

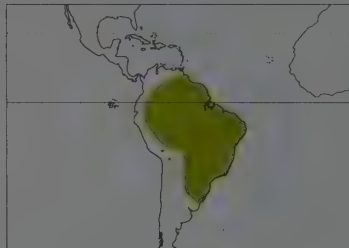
Calliphlox amethystina

French: Colibri améthyste **German:** Amethyststernkolibri **Spanish:** Colibrí Amatista

Taxonomy. *Trochilus amethystinus* Boddaert, 1783, Cayenne.

Occasionally treated as sole member of present genus; at the other extreme, genus considered to include all species of currently recognized genera *Tilmatura*, *Doricha*, *Microstilbon*, *Calothorax* and sometimes also *Thaumastura*, on grounds that females are very similar, males differing essentially in specialized details of plumage. Form "*C. orthura*" (Cayenne) may represent immature male of present species. Monotypic.

Distribution. E Colombia, S Venezuela and the Guianas through E Ecuador, NE Peru, N Bolivia and most of Brazil to Paraguay and NE Argentina (Misiones).



Descriptive notes. 6-6-6 cm; 2-3-2-5 g. Male has medium-sized, straight black bill; upperparts dark bronzy-green, postocular spot white, large white flank spot on either side of rump; gorget iridescent amethyst, whitish band across breast, rest of underparts greenish, with brownish lower flanks; tail deeply forked, purple-black, tipped green. Eclipse male has pale throat with some iridescent discs. Female has upperparts similar to male; underparts whitish, throat with a few green spangles, flanks and undertail-coverts rufous, white patch on either side of rump; tail short, mainly dull green, with black subterminal band, tipped

white to buff or cinnamon. Immature resembles adult female.

Habitat. A great variety of habitats from humid forest borders, clearings and savannas to scrubby open woodland, not present inside forests; up to 1500 m. Forages in low bushes and small trees.

Food and Feeding. Takes nectar of a great variety of flowers, including *Anacardium*, *Calliandra*, *Citrus*, *Convolvulus*, *Delphinium*, *Duranta*, *Erythrina*, *Fuchsia*, *Genipa*, *Grevillea*, *Helicteris*, *Inga*, *Lantana*, *Leonurus*, *Maranta*, *Nicotina*, *Palicourea*, *Passiflora*, *Pavonia*, *Psychotria*, *Sarantia*, *Stachytarpheta*, *Struthantus*, *Vochysia* and introduced *Eucalyptus* trees. Insects are caught in the air by hawking.

Breeding. Nov-Apr. Cup-shaped nest is built of soft plant material from *Typha*, Bromeliaceae and Gramineae, decorated outside with lichens, placed on a horizontal branch inside vegetation. Clutch size 2; incubation 13-14 days, by female; fledging at 20-22 days.

Movements. Probably mainly sedentary with some local dispersal, but poorly understood.

Status and Conservation. Not globally threatened. CITES II. Common in most of range; apparently rather local in Colombia, where not well known. Throughout range appears to accept man-made habitats like gardens and parkland. In NE Argentina, population appears to have declined, and species has now become the rarest of the regularly recorded hummingbirds in Iguazú National Park.

Bibliography. de Almeida & Ruschi (1976), Belton (1984), Best *et al.* (1997), Bloch *et al.* (1991), Bond & Meyer de Schauensee (1943), Butler (1979), Canevary *et al.* (1991), Cordier (1982), Donahue (1994), Gilliard (1941), Grantsau (1988), Haverschmidt & Mees (1994), Hayes (1995), Hellmayr (1929), Herzog *et al.* (1997), Hilty & Brown (1986), Meyer de Schauensee & Phelps (1978), Navas & Bo (1993), Oniki (1996), Parker *et al.* (1982), de la Peña (1994), Remsen & Traylor (1983, 1989), do Rosário (1996), Ruschi (1949a, 1949b, 1950a, 1962e, 1964c, 1964g, 1973b, 1973d, 1981-1982, 1986), Saibene *et al.* (1996), Sick (1993, 1997), Snyder (1966), Stotz *et al.* (1996), Taczanowski (1884), Tostain *et al.* (1992), Zimmer (1930, 1953a).

Genus MICROSTILBON Todd, 1913

302. Slender-tailed Woodstar

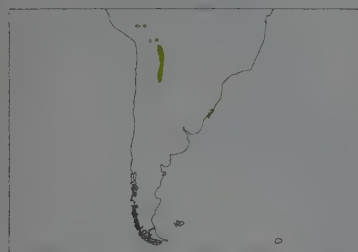
Microstilbon burmeisteri

French: Colibri de Burmeister **German:** Rotbart-Sternkolibri **Spanish:** Colibrí de Burmeister
Other common names: Slender-billed Woodstar

Taxonomy. *Chaetocercus burmeisteri* P. L. Sclater, 1887, Valle del Tafi, Tucumán, Argentina. Genus sometimes merged into an expanded version of *Calliphlox*; on the basis of morphological characters, however, probably best placed within *Chaetocercus*, as originally proposed. Monotypic.

Distribution. C & S Bolivia to N Argentina (Jujuy, Salta, Tucumán). Old record from Yungas of La Paz (NW Bolivia).

Descriptive notes. 7-9 cm (including tail of c. 3 cm). Male has short, rather straight black bill; upperparts bronzy-green; gorget reddish-purple, flaring into long moustachial tufts, bordered below by white; rest of underparts pale greyish, throat and sides mottled green, undertail-coverts pale cinnamon; very narrow black tail forked, with rectrices blunt-tipped. Eclipse male has pale throat. Female similar to male, cheeks dark, with small white postocular stripe; underparts cinnamon-buff



with white patch on either side of rump; tail short, square, central feathers green, rest cinnamon with black subterminal band. Immature resembles adult female.

Habitat. Shrubby slopes, ravines with vine-tangled thickets, and patches of deciduous woodland at 1600-2600 m.

Food and Feeding. Presumably takes insects and nectar from small flowers similar to those visited by *Chaetocercus*, recorded visiting flowering epiphytes. Forages at higher strata, with fast wingbeat giving the impression of a bumblebee; subordinate to other hummingbirds.

Breeding. No information available.

Movements. Seasonal altitudinal movements most likely.

Status and Conservation. Not globally threatened. CITES II. Generally not uncommon to common, but often overlooked due to its small size and retiring habits. Life history virtually unknown; available evidence suggests it may accept man-made habitats to some extent, but further investigation required. Presence in Yungas of La Paz documented by old specimen; no recent records in the area. Occurs in Calilegua National Park (Argentina).

Bibliography. Babarskas *et al.* (1995), Bond & Meyer de Schauensee (1943), Budin (1928), Burmeister (1890), Canevari *et al.* (1991), Fjeldså (1995), Fjeldså & Krabbe (1989, 1990), Fjeldså & Mayer (1996), Hartert (1902), Meyer de Schauensee (1982), Olrog (1968, 1984), de la Peña (1994), Remsen & Traylor (1989), Remsen, Traylor & Parkes (1986), Stotz *et al.* (1996), Todd (1942).

Genus CALOTHORAX G. R. Gray, 1840

303. Lucifer Hummingbird

Calothorax lucifer

French: Colibri lucifer

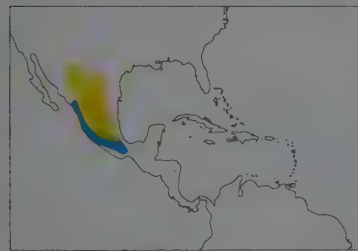
German: Luzifersternkolibri

Spanish: Colibri Lucifer

Taxonomy. *Cyananthus Lucifer* Swainson, 1827, Temascaltepec, Mexico.

Genus sometimes merged into an expanded version of *Calliphlox*. Forms a superspecies with *C. pulcher*; closely related to genus *Doricha*, which is sometimes united with present genus on the basis of similar morphological characters. Monotypic.

Distribution. CS USA (Arizona, W Texas) through C plateau of Mexico to Jalisco, Michoacan and Puebla. Winters from Nayarit E to Puebla and S to Oaxaca, irregularly N to Sinaloa.



Descriptive notes. 9-10 cm; 2.9-3.5 g. Medium-sized hummingbird with long, decurved, black bill; both sexes green above. Male has dull green forehead, rest of upperparts green; large iridescent gorget reflecting purplish-rose or magenta, elongated laterally, bordered by white on sides and below, rest of underparts green with small patch of rufous on lower flanks; tail long and forked, outer rectrices long, dark and narrow, with outermost pair sharply pointed at tip, central rectrices short, green. Female has curved bill; upperparts green; underparts pale buffy cinnamon, centre of belly white, sides of breast sometimes with

small green patches; tail double-lobed, inner rectrices green, outer ones cinnamon on outer webs and black distally with white tips. Immature resembles female, immature male develops some colour on throat in late summer.

Habitat. Arid scrub, canyons and lower mountain slopes. In N Chihuahuan Desert, found mainly in canyons and foothills of mountains rather than on open *bajadas*. Near Mexico City, originally common at lower elevations around 2200 m in cultivated areas, plains and volcanic hills. Winters mostly below 1800 m, but away from coast; the few descriptions of habitat include thorn forest, tropical deciduous forest and arid subtropical scrub.

Food and Feeding. Nectar from a variety of flowers; in Texas, takes nectar from mostly red-flowered herbs or shrubs such as *Penstemon havardii*, *Castilleja lanata*, or *Anisacanthus linearis*, but in midsummer exploits yellow-flowered century plant (*Agave havardiana*) for nectar not harvested by bats, doves, or orioles. In Mexico City, uses *Bouvardia caracasana*, *Erythrina corallodendron*, *Opuntia*, *Salvia mexicana*, *Mirabilis jalapa* and *Manfreda brachystachya*. Little is known concerning food plants used in winter and on migration. Flycatches for small flying insects using brief sallies from perch.

Breeding. Apr-Aug in Texas, but sometimes delayed until late May or Jun when summer rains begin; May-Sept at Mexico City. Nests sometimes aggregated, as many as 5 within radius of 200 m. Prefers nesting on rocky, sparsely vegetated slopes bordering lush canyon streams, almost never

using riparian vegetation. Common nest plants in Texas are dead flowering stalks of *Agave lechuguilla*, ocotillo (*Fouquieria splendens*) branches and chollas (*Opuntia imbricata*); in Mexico City, low shrubs or herbs such as jarilla (*Senecio salignus*), cardo santo (*Centaurea mexicana*), or chicalote (*Argemone mexicana*). Female takes 1 week or more to build cup-shaped nest, gathering cottony material if available, small leaves and flower heads, and binding with spider web. Clutch size 2; laying interval 2 days; incubation about 15 days, by female; chick naked for first 9 days except for down along back, pinfeathers appearing at 10-12 days; fledging period 19-24 days. Young remain near nest for 2-3 weeks, often in shrub thicket offering shade, and continue to be fed by female. 2 broods per year probably common at Mexico City, less so in Texas due to lean periods of flowering.

Movements. Breeding populations near Mexico City and along USA-Mexico border are migratory; status in E foothills of Sierra Madre Occidental and in C Chihuahuan Desert uncertain. In north, birds arrive early Apr, depart Sept; at Mexico City, arrive Mar-Apr, departing Oct-Nov. Destinations of these birds not known, but species winters mostly in interior C & SW Mexico at 800-1800 m, from Jalisco, Guanajuato and Querétaro S to Guerrero and Oaxaca; occasionally W to Sinaloa. In Sierra de Manantlán, Jalisco, a summer visitor at end of dry season (May-Jun). Birds captured in S Arizona Apr-Aug (rare), away from known breeding areas, may be wanderers or breeders whose nest-sites have not been found. Other populations not studied.

Status and Conservation. Not globally threatened. CITES II. Breeding range is large and a variety of xeric habitats appear to be acceptable. Preference, during breeding season in north, for arid, open, rugged habitats may afford protection, because such country is less apt to be altered by humans than are forests or riparian areas. In Mexico City region was once the most characteristic hummingbird, but no recent reports of status. Has persisted on NE edge of range since 1900 in Big Bend National Park, Texas, without expanding; estimated c. 50 females nest there annually. Increasingly observed in S Arizona, but still rare. Wintering habitats poorly known, and likewise their current suitability to support hummingbirds.

Bibliography. Arizmendi & Ornelas (1990), Baicich & Harrison (1997), Baltosser (1986a, 1989b), Bent (1940), Binford (1989), Carignan (1988), DeGraaf & Rappole (1995), Des Granges & Grant (1980), Ely (1962), Fleming & Baker (1963), Fox (1954), Friedmann *et al.* (1950), Hejl *et al.* (1995), Howell & Webb (1995a), Johnsgard (1997), Kaufman (1992, 1996), Kuban & Neill (1978), Kuban *et al.* (1983), Morales (1990), Navarro *et al.* (1991), Nelson (1970), Ornelas (1984), Pulich & Pulich (1963), Remsen, Stiles & Scott (1986), Ridgway (1911), Russell & Lamm (1978), Russell *et al.* (1994), Rutledge & Joseph (1981), Scott (1989, 1993, 1994a), Stotz *et al.* (1996), Taylor & Duvall (1951), Toledo (1974), Villada (1873), Vuilleumier & Williams (1964), Wagner (1946b, 1957b).

304. Beautiful Hummingbird

Calothorax pulcher

French: Colibri charmant

German: Schmucksternkolibri

Spanish: Colibri Bonito

Taxonomy. *Calothorax pulchra* Gould, 1859, Oaxaca, Mexico.

Genus sometimes merged into an expanded version of *Calliphlox*. Forms a superspecies with *C. lucifer*; closely related to *Doricha*, which is sometimes united with present genus on the basis of similar morphological characters. Monotypic.

Distribution. Interior of S Mexico, from C Guerrero and S Puebla SE to E Oaxaca. Also reported from Distrito Federal, Morelos and Chiapas, but identity of specimens doubtful.



Descriptive notes. 8-9 cm; 2.6-3.1 g. Very similar to *C. lucifer*, and almost inseparable in field. Male has bill less decurved, shorter and slender, black; dull green forehead, rest of upperparts green; large iridescent gorget reflecting purplish-rose or magenta, elongated laterally, bordered by white on sides and below, rest of underparts green with small patch of rufous on lower flanks; tail long and forked, outermost pair of rectrices broader and bluntly (rather than sharply) pointed. Female has variably curved bill, generally shorter and straighter than in *C. lucifer*; upperparts green; buff on throat and breast, no iridescent feathers, underparts similar to those of female

C. lucifer; tail double-rounded, inner rectrices green, outer ones rufous and black distally with white tips. Immature resembles female, immature male develops some colour on throat in late summer.

Habitat. Arid, semi-arid and subtropical scrub and thorn forest, high basins, usually between elevations of 1000 m and 2200 m.

Food and Feeding. Forages for nectar on low-growing *Erythrina*, *Salvia*, *Agave*, cacti and *Castilleja*. Flycatches for small flying insects in brief sallies from perch.

Breeding. One nest record in May. Nest cup-shaped, placed on a forked branch 2.5 m above ground, made of plant fibres, lined with plant down, outside decorated with brown Compositae pappi. Clutch size 2; incubation 15-16 days, by female; fledging period 19-22 days.

Movements. Sedentary. Occurs seasonally (Dec-Apr) to near sea-level in Isthmus of Tehuantepec.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Balsas Region and Interior Oaxaca EBA. Considered fairly common to common, but generally little known. Regularly recorded at Laguna San Felipe (C México) and Monte Albán (Oaxaca).

Bibliography. Anon. (1998a), Binford (1989), Brown & Bowers (1985), Davis (1972), Friedmann *et al.* (1950), Howell & Webb (1995a), Johnsgard (1997), Ridgway (1911), Rowley (1984), Stattersfield *et al.* (1998), Stotz *et al.* (1996).

Genus *MELLISUGA* Brisson, 1760

305. Vervain Hummingbird

Mellisuga minima

French: Colibri nain German: Zwergelfe Spanish: Colibrí Zumbadorcito

Taxonomy. *Trochilus minimus* Linnaeus, 1758, Jamaica.

Genus sometimes expanded to include all species currently placed in *Archilochus*, *Calypte* and *Stellula*; at other extreme, present species has often been treated as sole member of present genus. Two subspecies recognized.

Subspecies and Distribution.

M. m. minima (Linnaeus, 1758) - Jamaica.

M. m. vieillotii (Shaw, 1812) - Hispaniola and nearby islands of Gonâve, Tortue, Saona, Catalina and Vache.



Descriptive notes. 6-7 cm; male 2-7 g, female 3-6 g. Tiny, with dull metallic bronze-green upperparts and generally dull white underparts; bill is straight and dull black. Male has slightly concave tail, female is slightly larger with rounded tail, two outermost rectrices broadly tipped with white. Immature similar to female. Race *vieillotii* is darker, male with longer wings and more deeply forked tail.

Habitat. Open woodland, scrub, shrubbery and gardens, but absent from dense forest.

Food and Feeding. Nectar of *Pachystachys*, *Anacardium*, *Asclepias*, *Bourreria*, *Cordia*, *Lemaireocereus*, *Opuntia*, *Bauhinia*, *Caesal-*

pinia, *Delonix*, *Tamarindus*, *Laguncularia*, *Ageratum*, *Vaccinium*, *Croton*, *Plectranthus*, *Cuphea*, *Malvaviscus*, *Miconia*, *Acacia*, *Calliandra*, *Crotalaria*, *Plumbago*, *Securidaca*, *Cephaelis*, *Hamelia*, *Ixora*, *Morinda*, *Russelia*, *Dunalia*, *Holmskioldia*, *Lantana*, *Nyctanthes* and *Stachytarpheta* species.

Breeding. Nest-site often low down near the ground in bushes. Cup nest made of cottony fibres, with lichens, moss, bark, etc. Clutch size 2; incubation about 12 days, by female; fledging period 19-22 days.

Movements. No reliable information available. Presumably sedentary; accidental in Puerto Rico. **Status and Conservation.** Not globally threatened. CITES II. Restricted-range species: present in Jamaica EBA and Hispaniola EBA. Common throughout most of its extensive range, and readily observed in the open habitats of much of the Caribbean.

Bibliography. Anon. (1998a), Bond (1985), Curzon (1998), Danforth (1928, 1929), Dod (1987, 1992), Jeffrey-Smith (1966), Griswold (1960), Lack (1976), Raffaele *et al.* (1998), Rutgers & Norris (1972), Schuchmann (1980b, 1980c, 1990a), Schwartz (1997), Smith (1967), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Tyrrell & Tyrrell (1990), Wetmore (1936), Wetmore & Swales (1931).

306. Bee Hummingbird

Mellisuga helenae

French: Colibri d'Helen German: Bienenelfe Spanish: Colibrí Zuncuncito

Taxonomy. *Orthorhynchus helenae* Lembeye, 1850, Cárdenas, Cuba.

Genus sometimes expanded to include all species currently placed in *Archilochus*, *Calypte* and *Stellula*; in contrast, present species has often been transferred to genus *Calypte*. Monotypic.

Distribution. Cuba and I of Pines.



Descriptive notes. 5-6 cm; 1.6-1.9 g. Male is the smallest of all birds. Bill is straight and dull black; male has head and throat fiery red, and iridescent gorget with elongated lateral plumes; rest of upperparts bluish; rest of underparts mostly greyish-white; tail slightly concave. Female is slightly larger, upperparts green, underparts whitish; tail rounded and with white tips to outer tail feathers. Immature similar to female.

Habitat. Woodland, swampland, shrubbery and gardens; occasionally in fairly open country, but generally requires mature growth with thick tangles of lianas and rich in epiphytes.

Food and Feeding. Nectar of *Aloe*, *Laguncularia*, *Goethea*, *Hibiscus*, *Malvaviscus*, *Leucaena*, *Hamelia*, *Ixora*, *Russelia* and *Duranta* species; also reported to take nectar from flowers of the mangrove *Avicennia germinans*. During breeding, female observed feeding on *Seufamia diversifolia*, *Pavonia spicata*, *Calophyllum antillanum* and an *Oxidium* orchid. Also takes small insects; chicks left alone in nest while female forages will catch and eat small insects that come within range.

Breeding. Mar-Jun. Nest is generally situated c. 3-5 m (3-5) above the ground on a thin twig, typically of *Bucida buceras*, *Calophyllum antillanum* or *Nectandra coriacea*; made of dried plant fibres with a soft inner layer of plant wool, decorated on outside with lichens, and usually partly hidden by overhanging leaves; construction, by female, takes c. 10 days. Clutch size 2, with laying interval 1 day; incubation 21-22 days; naked, dark red chicks hatch asynchronously, 1 day apart; fed and brooded by female; have full set of feathers by 13-14 days old, and then perform flight exercises for 4-5 days; chicks leaving nest at c. 18 days old.

Movements. No reliable information available. Presumably sedentary as a rule, though recorded as vagrant to Providenciales (Caicos Is) and Bahamas.

Status and Conservation. Not globally threatened. CITES II. Currently considered Near-threatened. Population clearly in decline, presumably as a result of habitat loss, as species seems heavily

dependent on mature forest types. Formerly occurred throughout Cuba and I of Pines, but may now survive only at a few localities in Guanahacabibes, the Zapata Swamp, and the Cuchillas de Toa, though also recorded recently at Pinares de Mayarí and at other sites in province of Guantánamo. In Zapata Swamp, species restricted to areas of semi-deciduous forest, swamp-forest and mangroves. **Bibliography.** Anon. (1998a), Barbour (1943), Bond (1985), Collar & Andrew (1988), Collar *et al.* (1994), Garrido (1985), Garrido & García (1975), Martínez, O. *et al.* (1998), Mitchell & Wells (1997), Raffaele *et al.* (1998), Rodiles (1960), Rutgers & Norris (1972), Stotz *et al.* (1996), Tyrrell & Tyrrell (1990), Vaurie (1957), Wetmore (1936).

Genus *ARCHILOCHUS* Reichenbach, 1854

307. Ruby-throated Hummingbird

Archilochus colubris

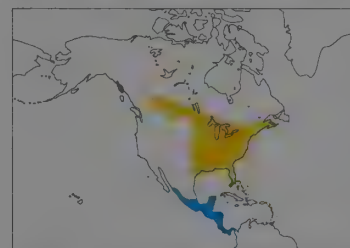
French: Colibri à gorge rubis German: Rubinkehlkolibri Spanish: Colibrí Gorgirrubí

Taxonomy. *Trochilus Colubris* Linnaeus, 1758, South Carolina.

Genus sometimes merged into *Mellisuga*; alternatively linked with *Selasphorus*. On occasion, considered to form a superspecies with *A. alexandri*; some authors would also include *Calypte costae*. Monotypic.

Distribution. S Canada (C Alberta E to Nova Scotia) and C & E USA (North Dakota E to Maine, and S to S Texas and Florida. Winters from C Mexico to W Panama, and also in S Florida (USA).

Descriptive notes. 9 cm; male 3-0 g, female 3-3 g. Small hummingbird, with long, thin dark bill. Male has upperparts iridescent green; white postocular spot; black line from lores back onto ear-coverts; iridescent red throat bordered below with white, remainder of underparts dusky greyish with greenish sides; wings dark; tail forked with outer rectrices greyish-brown, two central rectrices green; legs and feet are dark. Female like male but with chin and throat dusky or speckled white; tail is less forked with outer rectrices rounded and white at tips; cannot be safely distinguished from female *A. alexandri* except by bill measurements. Immature similar to female; most immature males (over 60%) show one or more ruby feathers in the throat region.



Habitat. Breeding habitat deciduous and mixed forest, parklands, second growth woodlands and gardens to 1500 m. Winters in wide range of tropical forest and scrub types, but principally in lowland dry forest and second growth to 1900 m.

Food and Feeding. Flowers of c. 30 species of plants have been identified as being used as temperate region nectar sources, most of which are red or orange in colour. The list of favoured plant genera includes *Campsis*, *Impatiens*, *Malvaviscus*, *Aesculus*, *Ribes*, *Aquilegia*, *Monarda* and *Macranthera*. Importance of a particular plant in the diet varies by season and locality. Genera of tropical plants known to be used as nectar sources include *Tabebuia*, *Convolvulus*, *Bombacopsis*, *Bumelia*, *Paullinia*, *Lobelia* and *Inga*. The proportion of the diet consisting of arthropods is not known. In some parts of the winter range, individuals arrive when few or no nectar resources are available, and must depend upon arthropod prey until some time after their arrival when dry season flowering occurs. Even when suitable flowers are available as much as 70% of the winter diet can be composed of arthropods. Flycatching is the principal foraging mode used to capture insect prey, though some are taken from flowers. Both intra- and inter-specific defence of resources are used under certain circumstances, evidently dependent on the type and distribution of the resource and the nature of the competitors.

Breeding. Male arrives on breeding territory from early Apr (S) to late May (N), 5-7 days prior to female; nesting normally lasts until Jul, exceptionally into Aug. Courtship involves an elaborate aerial display in which the male flies back and forth near the female in a half circle 2-3 m in radius, like a ball rolling in a bowl. Nest building begins from mid-Apr (S) to early Jun (N), and is done mostly by the female in a period of 4-5 days. The nest is a cup, 2-5 cm in diameter, constructed of plant material, lichens and spider web, with lichens plastered on the outside and a plant down lining; placed on a horizontal branch 4-5 m above the ground (range 1-5-15 m). Trees commonly used as nest-sites include *Quercus*, *Acer*, *Platanus* and *Fagus*. Male is polygynous, normally associating with the female only during courtship and egg-laying. Clutch size 2, laid at 1-day intervals; incubation about 16 days, beginning with last egg; fledging period roughly 15-20 days, though can be 28 days. Young are fed and cared for by the female for an unknown period after fledging. Re-nesting after failed attempts is common, but efforts to raise a second brood are unusual. A complete prebasic moult takes place on the wintering ground, lasting from late Sept or Oct to mid-Feb or Mar, ending with replacement of the gorget in males.

Movements. Migratory, wintering in C Mexico S to W Panama, and also in S Florida (USA); arrives on breeding grounds Apr and May, departs for wintering areas Aug and Sept, arriving Sept and Oct. Some authors have suggested that the principal migration route crosses the Gulf of Mexico; however, although many birds are found along the northern Gulf coast in spring, data documenting actual trans-Gulf flight, like mid-Gulf records from ships, observations of arriving birds in Yucatán, or grounding of trans-Gulf migrants by storms and headwinds, are few; recorded in Greater Antilles, Bahamas and Bermuda. Texas data indicate that a major portion of the population follows a circum-Gulf route in both autumn and spring.

Status and Conservation. Not globally threatened. CITES II. US National Breeding Bird Survey data show no significant range-wide, long-term change (1966-1994) in populations. Nevertheless, declines observed at a number of sites in the species' breeding range caused it to be listed during 1978-1986 by the National Audubon Society as a bird for which there were possible conservation concerns; local declines continue to be reported for many areas in E USA. Accurate breeding surveys are hard to obtain because this hummingbird is notoriously difficult to detect except at flowers or feeders. Very little is known about the bird's status during the non-breeding season. In Costa

On following pages: 308. Black-chinned Hummingbird (*Archilochus alexandri*); 309. Anna's Hummingbird (*Calypte anna*); 310. Costa's Hummingbird (*Calypte costae*); 311. Bumblebee Hummingbird (*Atthis heloisa*); 312. Wine-throated Hummingbird (*Atthis ellioti*); 313. Calliope Hummingbird (*Stellula calliope*); 314. Purple-collared Woodstar (*Myrtis fanny*); 315. Chilean Woodstar (*Myrtis yarrellii*); 316. Short-tailed Woodstar (*Myrtis micrura*).

Rica, occurs in several protected areas, e.g. Manuel Antonio, Santa Rosa, Palo Verde and Barra Honda National Parks.

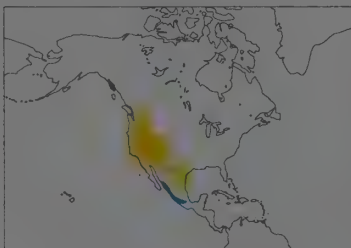
Bibliography. Allard (1934), Allen (1930), Arizmendi & Ornelas (1990), Austin (1975), Baicich & Harrison (1997), Baltosser (1987, 1995), Bass (1988), Baumgartner (1989a, 1989b), Bent (1940), Berkey (1988), Bertin (1980, 1982a, 1982b), Binford (1989), Brauning (1992), Buettner (1982), Butler (1949), Chapman (1924), Conway (1992), Cyr (1995), DeGraaf & Rappole (1995), Des Granges (1999), Des Granges & Grant (1980), Drazkowski (1984), Dunn *et al.* (1996), Duvic (1989), Ehrlich *et al.* (1992), Epp (1996), Eyer (1949), Feinsinger (1976, 1980), Foster & Tate (1966), Friedmann *et al.* (1950), Friesen (1987), Fye (1984), George (1980), Gessell (1934), Goertz *et al.* (1980), Graef (1991), Greenberg (1992), Griscom (1932a), Hanan (1995), Hauser & Currie (1966), Hildebrand (1949), Hilton (1990), Hinman (1928), Hooker (1990), Howell & Webb (1995a), James (1948), Johnsgard (1979, 1997), Johnson (1970), Kaufman (1996), Konrad (1996), Leberman (1972), Maslowski *et al.* (1992), Mayr (1966), Mayr & Short (1970), McGrath & Moss (1988), McKenzie (1991), Miller & Miller (1971), Miller & Nero (1983), Monroe (1968), Moore, E.V. (1981), Moore, F.R. *et al.* (1990), Mulvihill & Leberman (1987, 1992), Mulvihill *et al.* (1992), Murray (1958), Newfield (1996), Nice (1954), Nickell (1948), Norris *et al.* (1957), Norris-Elye (1944), O'Grady (1993), Odum *et al.* (1961), Olson & Olson (1985), Owen (1979), Payne (1984), Pickens (1927, 1930, 1944), Pickens & Garrison (1931), Pitelka (1942), Price *et al.* (1995), Pyle *et al.* (1997), Raffaele *et al.* (1998), Ramos (1974), Rappole (1978), Rappole & Blacklock (1985), Ricciardi (1996), Richardson (1993), Ridgely & Gwynne (1989), Ridgway (1892, 1911), Robinson *et al.* (1996), Root (1988), Rutgers & Norris (1972), Sargent & Sargent (1996a), Saunders, A.A. (1936), Saunders, W.E. (1942), Schenck (1980), Schlag (1930), Sealy (1986, 1989), Sherman (1913), Siegel & Centeno (1996), Slud (1964), Smyth (1990), Sorrie (1980), Southwick (1977), Southwick & Southwick (1980), Stevenson (1957), Stiles & Skutch (1989), Stotz *et al.* (1996), Tate (1986), Underwood (1896), Vacin (1970), Welter (1935), Wetherbee (1958), Wetherbee & Wetherbee (1961), Wetmore (1968a), Wetmore & Swales (1931), Whitten (1981), Whittle (1937), Willimont *et al.* (1988), Winker, Warner & Weisbrod (1992), Wolf (1970), Womack (1994), Wright (1962).

308. Black-chinned Hummingbird

Archilochus alexandri

French: Colibri à gorge noire **German:** Schwarzkinnkolibri **Spanish:** Colibrí Gorginegro
Other common names: Purple-throated Hummingbird

Taxonomy. *Trochilus Alexandri* Bourcier and Mulsant, 1846, Sierra Madre Occidental, Mexico. Genus sometimes merged into *Mellisuga*; alternatively linked with *Selasphorus*. On occasion, considered to form a superspecies with *A. colubris*; some authors would also include *Calypte costae*. "*Trochilus violajugulum*" is probably a hybrid of present species with *Calypte anna*. Monotypic. **Distribution.** SW Canada (British Columbia) S through W USA (E to E Texas) to N Mexico (N Baja California, NE Sonora to NW Tamaulipas). Winters in W & SC Mexico (S Sonora to N Guerrero and W Veracruz).



Descriptive notes. 10 cm: male 3-1 g, female 3-4 g. Small hummingbird with long, thin dark bill. Male has upperparts iridescent green; white postocular spot; lores and chin back onto ear-coverts black; throat iridescent violet, remainder of underparts white with greenish sides; wings dark; tail forked with outer rectrices greyish-brown; two central rectrices green; legs and feet dark. Female like male but with chin and throat a dusky or speckled white; tail is less forked with outer rectrices rounded and white at tips; cannot be safely distinguished from female *A. colubris* except by bill measurements. Immature similar to female.

male. Most immature males (over 80%) show one or more black or violet feathers in the gorget.

Habitat. Breeding habitat open deciduous and mixed woodlands, chaparral, thorn forest, arid scrub and desert riparian scrub to 2000 m. Resident and wintering bird; occur in riparian woodlands, tropical dry forest and second growth to 2000 m.

Food and Feeding. Flowers of 40 plant species have been identified as providing nectar as part of the temperate diet, including species from the genera *Penstemon*, *Anisacanthus*, *Agave*, *Nicotiana*, *Lonicera*, *Delphinium*, *Cercidium*, *Bumelia*, *Ungnadia*, *Cercis*, *Aesculus* and *Ipomopsis*. Importance of a particular plant in the diet varies by season and locality. The proportion of the diet made up of arthropods is not known. Flycatching is the principal foraging mode used to capture insect prey, mainly flies (Diptera) and mayflies (Ephemeroptera). Both intra- and inter-specific defence of resources are used under certain circumstances, evidently dependent on the type and distribution of the resource and the nature of the competitors.

Breeding. Male arrives on temperate breeding territory from late Mar (S) to late May (N), 5-7 days prior to female; nesting normally lasts into Jul or Aug. Courtship involves aerial displays in which the male flies back and forth near the female in a half circle 20-30 m in radius in pendulum fashion, or sometimes making a horizontal "figure of 8" in the air. The flight display is accompanied by a rapid chatter or trill, probably a vocalization (as opposed to wing noise), produced when the male is directly over the female. Nest construction begins from early Apr (S) to early Jun (N), and is done mostly by the female in 4-5 days. The nest is a cup, 2.5 cm in diameter, of plant down, lichens, bud scales, spider web, bark and leaf parts, yellow *Platanus* leaf hairs constitute the principal construction material in some areas. The nest is generally placed on the main shaft or fork of branches overhanging a creek or arroyo, 3-5 m above the ground (range 1-9 m). Trees and shrubs commonly used as nest-sites include *Quercus*, *Platanus*, *Rhus*, *Condalia*, *Proxopis* and *Celtis*. Male is polygynous, usually associating with the female only during courtship and egg-laying. Clutch size 2, laid at intervals of 1.5-2 days; incubation c. 15 days, beginning with last egg; fledging period 15-20 days, sometimes longer. Young fed and cared for by female for an unknown duration after fledging (probably 7-14 days). Efforts to raise a second brood have been reported for S Arizona, New Mexico and Texas. Nesting normally lasts into Jul or Aug. A complete prebasic moult is undergone on the wintering ground by both adults and immatures, beginning with their arrival in Aug or Sept and lasting until Feb or Mar, ending with replacement of the gorget in males. **Movements.** Migratory, wintering from N & C Mexico S to S Mexico (Guerrero, Morelos, Veracruz); arrives on temperate breeding grounds in Mar-May and departs for wintering areas by Jul or Aug, arriving Aug-Sept. Some populations in N Mexico (Baja California, Sonora, Tamaulipas) may be resident.

Status and Conservation. Not globally threatened. CITES II. There are US National Breeding Bird Survey data for this species only for a few western regions, in which no short-term or long-term changes of significance have been detected. However, given the difficulty of detecting the bird away from feeders, these data may not reflect the actual situation. The widespread practice of removal of vegetation along arroyos, streams and rivers in Arizona and Texas has raised concerns among some conservationists for populations of this species. Little information other than distributional notes are available on status during the non-breeding season.

Bibliography. Arizmendi & Ornelas (1990), Baicich & Harrison (1997), Bailey (1928), Baldrige (1983), Baltosser (1978, 1983, 1986a, 1987, 1989b, 1995, 1996), Banks & Johnson (1961), Bené (1940, 1941, 1945, 1947), Bent (1940), Bransfield (1984), Brown, B.T. (1992), Brown, J.H. *et al.* (1981), Burleigh & Lowery (1942), Calder (1981b), Campbell *et al.* (1990), Cody (1968), Cogswell (1949, 1962), DeGraaf & Rappole (1995), Demaree (1970), Dunn *et al.* (1996), Elliston (1995), Elliston & Baltosser (1995), Ewald (1985), Ewald & Bransfield (1987), Friedmann *et al.* (1950), George (1980), Goldsmith, K.M. & Goldsmith (1979, 1982), Goldsmith, T.H. *et al.* (1981), Grant & Grant (1968), Hainsworth & Wolf (1978), Hejl *et al.* (1995), Howell & Webb (1995a), Johnsgard (1997), Kaufman (1996), Kozma & Mathews (1997), Kuban *et al.* (1983), Lynch & Ames (1970), Mayr & Short (1970), Newfield (1996), Norton *et al.* (1982), Oberholser (1974), Phillips *et al.* (1964), Pimm (1978), Pitelka (1951b), Powers, D.R. & Conley (1994), Powers, L.R. *et al.* (1984), Price *et al.* (1995), Pyle *et al.* (1997), Pytte & Ficken (1994), Rappole & Blacklock (1985, 1994), Ridgway (1911), Rising (1965), Root (1988), Ross (1970), van Rossem (1945a), Rusch *et al.* (1996), Rutledge & Joseph (1981), Scott (1989), Short & Phillips (1966), Sorrie (1980), Spofford (1976), Stiles (1971a, 1976), Stotz *et al.* (1996), Stromberg & Johnsen (1990), Valone (1992), Wilbur (1987), Wolf & Hainsworth (1977), Woods (1927).

Genus CALYPTE Gould, 1856

309. Anna's Hummingbird

Calypte anna

French: Colibri d'Anna

German: Annakolibri

Spanish: Colibrí de Ana

Taxonomy. *Ornismya Anna* Lesson, 1829, San Francisco, California.

Genus often merged into *Archilochus*, and both have sometimes been subsumed into *Selasphorus*; however, in morphology, vocalizations and displays, members of present genus stand apart from the *Selasphorus-Archilochus* assemblage; alternatively, present genus sometimes merged into *Mellisuga*. Closely related to *C. costae*, with which has hybridized. Also hybridizes with *Lampornis clemenciae*; "*Selasphorus floresii*" usually reckoned to be hybrid of present species with *S. sasin*; "*Trochilus violajugulum*" probably hybrid of present species with *Archilochus alexandri*. Monotypic. **Distribution.** SW Canada (British Columbia) through W USA (E to S Arizona) to NW Mexico (NW Baja California). Winter range highly unsettled, species occurring irregularly S to N Sonora, SE to Gulf Coast of USA, and even N to SE Alaska; sporadically occurs much further E.



Descriptive notes. 10-11 cm; male 3.3-5.8 g, female 3.3-4.7 g. Male has short, straight, black bill; upperparts golden green; head and elongated lateral throat feathers iridescent deep rose red, underparts grey washed with green, undertail-coverts green, edged grey; central rectrices golden green, lateral tail feathers dark greenish-bronze. Female similar to male, head greyish, small white postocular spot, lacks iridescent rose red on head and throat, red discs on throat appear with age; median rectrices golden green, rest blackish, outermost feathers tipped white. Immature similar to adult female.

Habitat. Chaparral, oak woodland, canyon bottoms, open woodland with evergreen broadleaf trees, riparian woodland, savanna-like vegetation, coastal shrub, urban and suburban environments, at sea-level to 1800 m. Forages in low to high strata, usually at 2-8 m.

Food and Feeding. Nectar of flowering native and introduced perennials, shrubs and trees, including *Ribes*, *Diaplasia*, *Salvia*, *Keckia*, *Aquilegia*, *Mimulus*, *Tecomaria*, *Kniphofia*, *Agave* and *Eucalyptus*. Male occupies feeding territories at nectar-rich sources. Insects are caught in the air by hawking or taken from foliage. Small flies constitute almost half of the arthropod consumption.

Breeding. Nov-May, occasionally to Jul. Cup-shaped nest constructed of soft material such as plant down, feathers, hair, held together by spider web and insect cocoon fibres and sometimes rodent hairs; on external wall decorated with lichen, moss, pieces of dead leaves and bark; placed on horizontal twigs, usually 2-6 m, sometimes up to 20 m above ground. Clutch size 2; incubation 14-19 days, by female; chick black with two dorsal rows of dull greyish down; fledging period 18-26 days. First breeding in second year.

Movements. Extensive post-breeding wandering. In recent years the species has considerably expanded its range of winter occurrence in USA towards SE. Recently recorded for first time in San Luis Potosí (NC Mexico).

Status and Conservation. Not globally threatened. CITES II. Generally common throughout range, and at present apparently in process of expansion. Populations benefit from introduced exotic plants and feeders provided by man. Readily accepts man-made habitats like suburban gardens and city parks.

Bibliography. Arnold (1930a, 1930b), Baicich & Harrison (1997), Baldrige *et al.* (1983), Baltosser (1987), Banks & Johnson (1961), Banks & Medina (1963), Baptista & Matsui (1979), Baptista & Schuchmann (1990), Bartholomew & Lighton (1986), Bartholomew *et al.* (1957), Bené (1947), Bent (1940), Berlioz (1930b), Beuchat *et al.* (1979), Bowles (1910), Bransfield (1984), Brice (1992), Brice *et al.* (1989), Calder (1974a), Collins & Collins (1968), Collins (1978), Campbell *et al.* (1990), Carpenter & Castonova (1980), Clark, F.C. (1902), Clyde (1972), Cogswell (1962), Davis (1997), Des Lauriers (1994), Dyer (1936), Eberhard & Ewald (1994), Ewald & Bransfield (1987), Ewald & Carpenter (1978), Ewald & Orians (1983), Gander (1927), Goldberg & Ewald (1991), Grant, K.A. & Grant (1967), Grant, V. & Grant (1966), Graves & Newfield (1996), Hamilton (1965), Harris-Haller & Harris (1991), Hejl *et al.* (1995), Howell, S.N.G. & Webb (1992b, 1995a), Howell, T.R. & Dawson (1954), Johnsgard (1997), Kaufman (1996), Kelly (1955, 1956), des Lauriers (1994), Legg & Pitelka (1956), Long (1993), Maender *et al.* (1996), Mayr & Short (1970), Meriées (1982), Miller (1940), Miskys (1976), Ortiz (1980), Pearson (1954), Phillips, A.R. (1947), Pitelka (1942, 1951a, 1951b), Powers (1987, 1988, 1991, 1992), Powers & Conley (1994), Powers & Nagy (1988), Price *et al.* (1995), Prill (1985), Pyle *et al.* (1997), Ridgway (1911), Rodgers (1940), Root (1988), van Rossem (1945a), Russell (1996), Rutgers & Norris (1972), Schmidt (1976), Schuchmann (1979d), Smith, W.K. *et al.* (1974), Stiles (1971b, 1973, 1976, 1982), Stoner (1946), Stott (1951), Taylor & Kamp (1985), Trousdale (1954), Udvardy (1983), Verbeek (1971), Vleck (1981), Welker (1984), Wells & Baptista (1979b), Wells, Baptista *et al.* (1996), Wells, Bradley & Baptista (1978), Wheeler (1980), Williamson (1956, 1957), Withers (1977a), Woods (1931), Yeaton & Laughlin (1976), Zimmerman (1973).

310. Costa's Hummingbird

Calypte costae

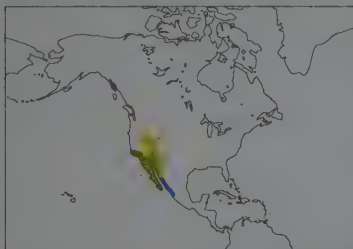
French: Colibri de Costa

German: Veilchenkopfele

Spanish: Colibrí de Costa

Taxonomy. *Ornismya Costae* Bourcier, 1839, Magdalena Bay, Baja California, Mexico. Genus often merged into *Archilochus*, and both have sometimes been subsumed into *Selasphorus*; however, in morphology, vocalizations and displays, members of present genus stand apart from the *Selasphorus-Archilochus* assemblage; alternatively, present genus sometimes merged into *Mellisuga*. Some authors would even place present species in the *Archilochus* superspecies. However, species is closely related to *C. anna*. Has hybridized with several other species of western North American hummingbirds, including *C. anna*, *Selasphorus platycercus*, *Lampornis clemenciae*, *Stellula calliope* and *Archilochus alexandri*. Monotypic.

Distribution. SW & WC USA (from C California, S Nevada and extreme SW Utah) S to NW Mexico (to S Baja California and C Sonora). Winters S to WC Mexico (at least to Nayarit).



Descriptive notes. 7.5-8.5 cm; male 3-0 g, female 3-3 g. Male has short, straight, black bill; crown and laterally elongated gorget brilliant metallic violet; rest of upperparts rather dull bronzy-green, including central rectrices; lateral rectrices greyish more or less glossed bronzy, the outermost greatly attenuated; foreneck greyish-white, centre of breast and belly pale grey passing to greenish-bronze scaled with greyish-buff laterally. Female lacks brilliant crown and gorget, sometimes with a few purple feathers on the centre of the throat; upperparts as in male, crown duller, often brownish; dull whitish on chin and

throat, pale greyish to greyish-brown below, vent and undertail-coverts whitish; central rectrices bronze-green narrowly tipped black; outer 3 dull greyish basally with black subterminal band and white tips. Immature very white below with pale buffy to whitish feather fringes over most of the upperparts, especially on the crown, nape and rump; young male often shows some dusky-grey or purple on the throat, but the purple feathers are more scattered and often occur near the corners of the future gorget, rather than being concentrated in a small central spot as in adult female; young female lacks purple but the throat is sometimes tinged with buff; outer rectrices of young male relatively longer than in adult female, giving the tail a double-lobed shape, rather than rounded.

Habitat. Desert, semi-desert, sagebrush scrub, dry open chaparral and coastal sage, oak savanna and brushy foothills. In desert, most numerous along dry washes; in chaparral and coastal sage prefers open south- or west-facing slopes. Breeding male prefers open areas with scattered tall shrubs or small trees, where flowers of herbs and small shrubs are abundant; female nests in similar habitats, sometimes in or near male territories. During nonbreeding season may occur in open meadows and gardens or citrus orchards. Avoids shaded or wooded areas, does not move into mountains following breeding as do some other hummingbirds of W USA; rarely occurs much above 1000 m.

Food and Feeding. In chaparral, coastal sage and oak savanna, preferred nectar flowers are usually species of *Salvia*, also *Trichostema*, *Ribes*, *Diplacus* and *Penstemon*; in desert and semi-desert areas visits especially flowers of *Beloperone*, *Delphinium* and *Isomeris*, sometimes *Fouquieria*, *Chilopsis*, *Lycium*, *Lotus*, *Phacelia* and *Hypsis*. Many of these are primarily insect-pollinated; *Fouquieria* may be pollinated more by orioles. During breeding season, male defends flowers in the vicinity of lookout perch, and may defend feeding territories at other seasons. Frequently takes small flies, gnats and wasps by hawking from perch or hovering and darting in swarms of Diptera over shrubs; also gleans from foliage, often inside shrubs in desert, for spiders and other arthropods.

Breeding. Feb-Jun (peak of egg-laying late May) in Baja California. Feb-Apr (late Feb-early Mar) in the Colorado Desert of California. Mar-Jul (late May-early Jun) in coastal chaparral and sage. Male occupies breeding territories as early as early Feb (deserts) or late Feb (chaparral). Nest a rather shallow cup of fine plant fibres and down, also spider web, often lined with small feathers and profusely decorated on outside with bits of lichen and bark, small dead leaves, seed heads or other plant matter, the overall tone being a mottled grey; placed 0.5-3 m above ground in outer foliage of a shrub, small tree or spiny cactus adjacent to an open space, giving the sitting female a clear view; rarely to 10 m in a tree. Clutch size 2, laying interval 2 days; incubation 15-16 days, by female; chick naked with rows of yellowish down on back; fledging at 20 days. Young remains near nest and fed by female for at least one more week. Possibly breeds in first year. In S California at least, a first brood may be raised in Colorado Desert and a second in chaparral.

Movements. Partial migrant, withdrawing from N part of breeding range, and concentrating in S part and somewhat beyond, in Mexico; winters mainly from S California and S Arizona to S Baja California and N Sinaloa. Following breeding some individuals disperse to N as far as extreme SW Canada and E as far as E Texas.

Status and Conservation. Not globally threatened. CITES II. Its dry, open habitats have on the whole suffered less impact from man than more mesic habitat types, and the species remains common over most of its range; common to fairly common in Mexico.

Bibliography. Austin (1970c), Avery & van Riper (1993), Baicich & Harrison (1997), Bakus (1962), Baltosser (1986a, 1987, 1989a, 1989b), Baltosser & Scott (1996), Banks (1963), Banks & Johnson (1961), Bené (1947), Bent (1940), Blake (1984), Brice & Grau (1991), Cardiff & Remsen (1981b), Carpenter & Hixon (1987), Cody (1968), Cogswell (1962), Crosswhite & Crosswhite (1981), DeGraaf & Rappole (1995), Dixon (1912), Fleming *et al.* (1996), Friedmann *et al.* (1950), Gault (1885), George (1987a, 1987b), Grant & Grant (1968), Grinnell & Miller (1944), Hejl *et al.* (1995), Hixon & Carpenter (1988), Howell & Webb (1995a), Huey (1944), Johnsgard (1997), Kaufman (1996), Lasiewski (1963), des Lauriers (1994), Mayr & Short (1970), Miller & Stebbins (1964), Palmer (1918), Phillips (1982), Phillips & Amadon (1952), Phillips *et al.* (1964), Pitelka (1951b), Powers (1988, 1991), Price *et al.* (1995), Pyle *et al.* (1997), Remsen, Stiles & Scott (1986), Ridgway (1911), Root (1988), van Rossem (1945a), Rothschild (1927), Scott (1989, 1994b), Short & Phillips (1966), Stiles (1971a, 1973), Stotz *et al.* (1996), Vleck (1981), Wagner (1957b), Waser (1979), Weathers (1983), Wells *et al.* (1978), Woods (1923, 1927, 1934).

Genus ATTHIS Reichenbach, 1854

311. Bumblebee Hummingbird

Atthis heloisa

French: Colibri h  loise

German: Rosenkehl  fe

Spanish: Colibr   de Eloisa

Other common names: Heloise's/Morcom's Hummingbird

Taxonomy. *Ornismya Heloisa* Lesson and DeLattre, 1839, Jalapa and Coatepec, Veracruz.

Genus probably closely related to *Selasphorus*, and sometimes merged into it. Forms a superspecies with *A. ellioti*, with which has been considered conspecific; however, they differ in courtship behaviour, song structure, wing morphology, and coloration, and thus merit treatment as separate species. Proposed race *morcomi*, known by two old specimens from SE Arizona, is synonym of nominate; presumably based on vagrants, or mislabelled specimens. Two subspecies recognized.

Subspecies and Distribution.

A. h. margarethae R. T. Moore, 1937 - highlands of NW & W Mexico (SE Sinaloa and SW Chihuahua to Jalisco).

A. h. heloisa (Lesson & DeLattre, 1839) - highlands of NE, C & S Mexico (C Tamaulipas to Guerrero and Oaxaca).



Descriptive notes. 7-7.5 cm; 2-2.7 g. Male has short, straight, black bill; upperparts green, white postocular stripe, greyish auriculars; gorget elongated at sides, rosy pink with some violet-blue highlights; underparts whitish with light cinnamon flanks mottled green; tail rounded, central pair of rectrices green, remainder rufous with black subterminal bar, outer 3 pairs tipped white. Female similar to male, has postocular spot white; throat whitish with greyish discs; tail double-lobed. Immature resembles adult female, immature male with some pinkish discs on throat. Male of race *margarethae* has gorget darker, less elongated, more

extensive white on underparts.

Habitat. Humid to semi-humid forest edges, pine and pine-oak woodland and clearings at 1500-3000 m. Forages from low to middle strata.

Food and Feeding. Feeds on nectar of flowering *Erythrina*, *Opuntia*, *Salvia*, *Cuphea jorullensis*, *Penstemon perfoliatus*, *P. gentianoides* and *Rigidella orthantha*; takes small arthropods. Does not establish feeding territories, and is subordinate to larger hummingbirds, but bumblebee-like flight allows it to forage in territories of other species without being noticed.

Breeding. Birds in breeding condition Apr-Jul. No further information available.

Movements. Sedentary, with occasional northward dispersal; old records from SE Arizona (USA), though possible implications unclear.

Status and Conservation. Not globally threatened. CITES II. Common throughout range. Seems to accept disturbed areas like clearings to some extent. Regularly recorded at Cerro de San Juan (Nayarit), Volc  n de Fuego (Jalisco), Sierra de Atoyac (Guerrero) and Cerro San Felipe and Valle Nacional (Oaxaca).

Bibliography. Anon. (1998a), Arizmendi *et al.* (1996), Bangs (1927), Bent (1940), Bertioz (1932b, 1938), Binford (1989), Contreras-Balderas (1997), Des Granges & Grant (1980), Edwards (1982), Friedmann *et al.* (1950), Griscom (1932c), Howell & Webb (1995a), Johnsgard (1997), Lowery & Dalquest (1951), Lyon (1976), Miller (1985), Moore (1937), Phillips (1975), Ridgway (1911), Robins & Heed (1951), Schaldach (1963), Stotz *et al.* (1996), del Toro (1941), Wagner (1946a), Wilson & Ceballos-Lascu  n (1993), Zyskowski *et al.* (1998).

312. Wine-throated Hummingbird

Atthis ellioti

French: Colibri d'Elliot

German: Elliotelfe

Spanish: Colibr   de Elliot

Taxonomy. *Atthis ellioti* Ridgway, 1878, Volc  n de Fuego, Guatemala.

Genus probably closely related to *Selasphorus*, and sometimes merged into it. Forms superspecies with *A. heloisa*, with which has been considered conspecific; however, they differ in courtship behaviour, song structure, wing morphology, and coloration, and thus merit treatment as separate species. Two subspecies recognized.

Subspecies and Distribution.

A. e. ellioti Ridgway, 1878 - highlands of S Mexico (Chiapas) and Guatemala.

A. e. selasphoroides Griscom, 1932 - highlands of Honduras.



Descriptive notes. 6.5-7 cm; 2-2.6 g. Very similar to *A. heloisa*. Male has short, straight, black bill; upperparts green, postocular stripe whitish, auriculars greyish; throat iridescent rose pink, rest of underparts whitish, flanks cinnamon mottled green; tail rounded, central pair of rectrices green, rufous distally, remainder rufous with black subterminal bar, outer rectrices tipped white to washed cinnamon. Female similar to male, postocular spot white; throat whitish with greyish discs, below whitish, flanks and undertail-coverts deep cinnamon; tail double-lobed, similar to male's. Immature resembles adult female, immature

male with some pinkish discs on throat. Male of race *selasphoroides* is more buff below, white tips on rectrices replaced by buff, subterminal bar broader.

Habitat. Humid to semi-humid forest edges, pine and pine-oak woodland and clearings at 1500-3500 m. Forages from low to middle strata.

Food and Feeding. Presumably feeds on a similar variety of floral nectar as *A. heloisa*. Visits *Erythrina*, *Opuntia*, *Salvia*, *Cuphea jorullensis*, *Penstemon perfoliatus*, *P. gentianoides* and *Rigidella orthantha*; takes small arthropods. Does not establish feeding territories, and is subordinate to larger hummingbirds, but bumblebee-like flight allows it to forage in territories of other species without being noticed.

Breeding. One record of a nest 1 m above the ground containing two chicks in Aug (Guatemala). Neither chicks nor nest have been described. No further information available.

Movements. Sedentary.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in North Central American Highlands EBA. Common throughout range. Seems able to adapt to some extent to disturbed areas like clearings. Regularly recorded in El Triunfo Biological Reserve and at Lagos de Montebello (S Chiapas).

Bibliography. Anon. (1998a), Baepier (1962), Bent (1940), Bertioz (1938, 1939), Dickey & van Rossem (1938), Eisenmann (1955), Friedmann *et al.* (1950), Griscom (1932c), Herm  ndez-Ba  os *et al.* (1995), Howell & Webb (1995a), Johnsgard (1997), Land (1970), Monroe (1968), Stotz *et al.* (1996), Thurber *et al.* (1987), Zyskowski *et al.* (1998).

Genus *STELLULA* Gould, 1861

313. Calliope Hummingbird

Stellula calliope

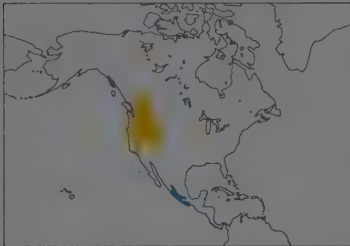
French: Colibri calliope

German: Sternelfe

Spanish: Colibrí Calíope

Taxonomy. *Trochilus (Calothorax) Calliope* Gould, 1847, Real del Monte, Hidalgo, Mexico. Genus sometimes merged into *Mellisuga*; alternatively lumped into *Archilochus*. Proposed race *lowei* (Guerrero) based on a winter specimen, and claimed differences fall within normal variation. Monotypic.

Distribution. SW Canada (C & E British Columbia and SW Alberta) and W USA in Rocky Mts and Sierra Nevada (Washington to California and E to Wyoming and W Colorado). Winters in WC & SC Mexico (SE Sinaloa to EC Oaxaca).



Descriptive notes. 6.9-7.4 cm; male 2.3-4 g, female 2.6-4 g. Male has straight black bill; upperparts shining bronzy-green; underparts white, gorget divided into magenta rays individually emphasized in star-burst; tail purplish-brown. Female similar to male, throat white with brown discs. Immature resembles adult female.

Habitat. Generally cool montane environments, with temperature range of 0.5-25°C. Breeds at elevations of from 180 m along Columbia R to timberline at 3000-3400 m in Sierra Nevada, California. On W slope of Oregon Cascade Mts, forages in grass-forb stage (1-7

years after deforestation by fire or logging) but prefers shrub-sapling stage (8-15 years) for nesting. In winter in thorn forest and shrubs in old burnt areas, at farm and ranch edges, and through transition zone of arid and humid pine-oak in W Mexico.

Food and Feeding. Nectar from red tubular "hummingbird flowers" and wide variety of yellow, white, blue and purple flowers. Aerial foraging for small flies (Diptera). Hymenoptera and beetles. Flower species visited include *Aquilegia elegantula*, *A. formosa*, *Arctostaphylos nevadensis*, *Berberis repens*, *Castilleja austromontana*, *C. breweri*, *C. linariaefolia*, *C. miniata*, *C. paysonae*, *Cleome serrulata*, *Corydalis caseana*, *Cynoglossum officinale*, *Delphinium nuttallianum*, *Epilobium alpinum*, *Ipomopsis aggregata*, *Lithospermum ruderale*, *Lonicera ciliosa*, *Mimulus lewisii*, *Monardella odoratissima*, *Pedicularis semibarbata*, *Penstemon barbatus*, *P. leiophyllus*, *P. menziesii*, *P. newberryi*, *Ribes cereum*, *Sarcodes sanguinea*, *Symphoricarpos oreophilus*, *S. albu*, *Viguiera multiflora* and *Salvia*. In Jalisco winter quarters, this hummingbird is subordinate to larger and resident species, feeding only at cup-shaped flowers or isolated tubular flowers not sought by other birds. Competition is not limited to hummingbirds: flocks of Orange-crowned Warblers (*Vermivora celata*) often heavily dusted with pollen in late Jan when *Senecio angulifolius* is among the most abundant flowers and used extensively by migrant trochilids, suggesting competition for food resources also with passerines.

Breeding. May-Jul. Nest cup-shaped, in conifer, apple, or alder, 2-12 m above ground, beneath overhanging branch which shields from cold sky radiation loss, precipitation and predation. Often built upon old pinecone base, lined and insulated with downy plant material, exterior layer of lichens, moss, or bark fragments anchored with strands of spider web. Materials may be robbed from nests of other species. Clutch size 2; incubation 15-16 days, by female; fledging period 18-21 days.

Movements. Site-fidelity indicated by recaptures of ringed birds. Migrates up to 4500 km to winter in Mexico (Sinaloa, Durango and Jalisco S to Guerrero and Oaxaca); accidental in SE USA. This species, migrant *Selasphorus rufus*, and resident *Calypte costae* held non-overlapping territories in Mar-Apr in the Mojave Desert, California, migrants taking space and resources which could have met breeding needs of other *C. costae*.

Status and Conservation. Not globally threatened. CITES II. Generally common. Selects early shrub stages after clear-cutting. Long-term effects of deforestation due to climatic changes (moisture and seasonal phenology) unknown. Density during breeding season in post-logging succession at least 3-6 birds/km². Trends unclear in both Canada and USA; some indications of declines, but most lack statistical significance. Management needs are not known; nor does conservation action seem necessary, unless herbicides and insecticides used in forest management are having an impact as yet unreported.

Bibliography. Armstrong (1986, 1987, 1988a, 1988b), Atwood (1979), Austin (1970b), Baicich & Harrison (1997), Baltosser (1987, 1994), Banks & Johnson (1961), Bent (1940), Berlioz (1930b), Binford (1989), Brown & Kodric-Brown (1979), Brunton *et al.* (1979), Burgoon *et al.* (1987), Burleigh (1972), Calder (1971, 1973a, 1974b), Calder & Calder (1994, 1995), Campbell & Hosford (1979), Campbell *et al.* (1990), Cody (1968), DeGraaf & Rappole (1995), Des Granges (1979), Des Granges & Grant (1980), Duffield (1972), Dunning (1993), Friedmann *et al.* (1950), Gabrielson & Jewett (1940), Godfrey (1986), Grant & Grant (1968), Graves & Newfield (1996), Grinnell & Miller (1984), Heidcamp (1997), Hejl *et al.* (1995), Howell & Webb (1995a), Johnson (1997), Kaufman (1996), Krebs (1997), Kuban & Neill (1980), Mailliard (1921), Marcot (1984), Martin (1988), Mayr & Short (1970), Meslow & Wright (1975), Mewaldt & Kaiser (1988), Newfield (1984, 1992), Ortiz (1972), Peterson & Chalif (1989), Phillips (1966, 1975), Pitelka (1942), Price *et al.* (1995), Pyle *et al.* (1997), Ridgway (1911), Rothschild (1927), Sargent & Sargent (1991), Stiles (1971a), Stotz *et al.* (1996), Tamm *et al.* (1989), Thayer & Bangs (1907), Tucker (1955), Wagner (1957b), Weydemeyer (1927, 1971), Wyman (1920).

Genus *MYRTIS* Reichenbach, 1854

314. Purple-collared Woodstar

Myrtis fanny

French: Colibri fanny

German: Türkischehlfe

Spanish: Colibrí Myrtis

Other common names: Fanny's Woodstar

Taxonomy. *Ornismya Fanny* Lesson, 1838, Peru.

Relationships unclear; eclipse plumage of adult male may indicate close affinities to *Calliphlox* and *Thaumastura*; some researchers postulate close links to North American genera *Calypte* and *Stellula*; present species often treated as sole member of *Myrtis*. Two subspecies recognized.

Subspecies and Distribution.

M. f. fanny (Lesson, 1838) - W & SE Ecuador to W Peru (Piura S to Arequipa).

M. f. megalura Zimmer, 1953 - N Peru (Cajabamba through SE La Libertad to extreme NW Huánuco).



Descriptive notes. 7.5-8 cm; 2.3-2.5 g. Male has short, slightly decurved black bill; upperparts bronze-green; throat and sides of neck iridescent aquamarine, bordered below by shining violet band, rest of underparts dirty white; tail long, deeply forked, dusky brown with light green gloss. Female above like male; underparts buffy, white on throat and centre of belly; tail short, rounded, central tail feathers blue-green, next pair tipped black, remainder black, tipped white. Immature like adult female. Race *megalura* differs from nominate by longer tail.

Habitat. Arid and semi-arid coastal scrub,

in Ecuador most numerous at 1000-2000 m. **Food and Feeding.** Nectar of flowering Malvaceae, cacti, *Cordia* and *Russelia*. Both sexes are trap-liners for nectar along fairly constant routes. Insects are caught in the air.

Breeding. Mar-Jun in Ecuador, Jun-Oct in Peru. Tiny cup-shaped nest of fine plant fibre and spider web is built in the fork of thin branches, 2-4 m above the ground, occasionally higher. Clutch size 2; incubation 15-16 days, by female; chick is black with grey dorsal down; fledging period 19-22 days. First breeding in second year.

Movements. Not known, but altitudinal movements most likely.

Status and Conservation. Not globally threatened. CITES II. Common resident from the coastal lowlands to higher altitudes; readily accepts man-made habitats like gardens and cultivated areas.

Bibliography. Best *et al.* (1997), Bloch *et al.* (1991), Butler (1979), Fjeldså & Krabbe (1990), González & Málaga (1997), Koepeke (1970), Meyer de Schauensee (1982), Olrog (1968), Parker *et al.* (1982), Ruschi (1964b, 1964h), Stotz *et al.* (1996), Taczanowski (1884), Taylor (1995), Williams & Tobias (1994), Zimmer (1930, 1953a).

315. Chilean Woodstar

Myrtis yarrellii

French: Colibri d'Arica

German: Aricaelfe

Spanish: Colibrí de Arica

Other common names: Yarrell's Woodstar

Taxonomy. *Trochilus Yarrellii* Bourcier, 1847, Montevideo; error = Arica, Chile.

Relationships unclear; usually placed in monotypic genus *Eulidia*, but external morphology and behaviour support treatment within *Myrtis*. Monotypic.

Distribution. S Peru (Tacna) and N Chile (near Arica, irregularly S to Antofagasta).



Descriptive notes. 7.5-8 cm; 2.3-2.6 g. Male has short black bill; upperparts iridescent olive green; throat shining violet-red, underparts white; central tail feathers very short, green, outer ones longer, blackish-brown. Female like male above, white tinged buff below; central rectrices green, outer tail feathers black, buff at the base with broad white tips. Immature probably similar to female.

Habitat. Cultivated desert river valleys and gardens from 200 m to 700 m, commonest below 400 m; one record at 2600 m.

Food and Feeding. Nectar of flowering *Lantana*, *Hibiscus*, shrubs, cacti and Leguminosae trees such as *Inga feulles*. Insects are caught on the wing.

Breeding. Little known. Nesting records refer to Aug and Sept. One immature was collected in Nov, suggesting a breeding season of Aug-Nov, possibly into Dec.

Movements. Presumably sedentary for the most part, occasionally straggling S into N Antofagasta, Chile; may be merely visitor to S Peru (Tacna).

Status and Conservation. VULNERABLE. CITES II. Restricted-range species; present in Peru-Chile Pacific Slope EBA. A little known species with a very limited distribution. In Peru, appears to be generally uncommon; present in gardens of Tacna city, and also in vegetation around nearby airport. In Chile, mainly restricted to Tarapacá, where locally common in lower sections of Lluta Valley and also in Azapa Valley; vegetation of both valleys has been heavily modified, with extensive planting of olive and citrus groves, but present species appears to survive with relatively healthy populations in both. In general, indigenous food plants of the species may have declined on a large scale when its habitat was converted to agricultural land; it now seems to depend largely on introduced garden flowers. Dominated in Chile by recently arrived *Thaumastura cora*, and this competition could prove a major problem to present species.

Bibliography. Araya & Chester (1993), Barros (1954), Bond & Meyer de Schauensee (1943), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Fjeldså & Krabbe (1990), Hellmayr (1932), Inskipp (1987), Johnson (1967, 1972), King (1978/79), McFarlane (1975), Parker, T.A. (1982), Parker, T.A. *et al.* (1982), Philippi (1936), Philippi *et al.* (1944), Remsen & Traylor (1989), Stattersfield *et al.* (1998), Stephens & Traylor (1983), Stotz *et al.* (1996), Wege & Long (1995), Zimmer (1953a).

Genus *MYRMIA* Mulsant, 1876

316. Short-tailed Woodstar

Myrmia micrura

French: Colibri à queue courte

German: Kurzschwanzelfe

Spanish: Colibrí Colicorto

Taxonomy. *Calothorax micrurus* Gould, 1854, Peru.

Affinities unclear; based on external morphology, seems to be closest to genus *Chaetocercus*, and sometimes placed therein. Monotypic.

Distribution. W Ecuador (S from Manabí and I La Plata) to NW Peru (S to La Libertad).

Descriptive notes. 6-6.5 cm; 2.7-3.3 g. Male has short, slightly decurved black bill; upperparts shining olive green; chin white, throat iridescent violet to turquoise, rest of underparts white; tail very short, feathers narrow and stiff, central tail feathers green and shorter than blackish outer ones. Female above like male; throat and breast cinnamon-buff, belly buffy grey; central tail feathers olive green, rest black, tipped white. Immature similar to adult female; immature male has median rectrices slender and pointed at tips, whereas those of female are broader and more evenly rounded.

Habitat. Occurs in coastal arid scrub vegetation, in dry valleys and gardens; most numerous below 200 m; forages at 1-3 m above ground.

Food and Feeding. Nectar of flowering Malvaceae shrubs, Cactaceae, Fabaceae and Caesalpinaceae (Leguminosae). Small insects are caught in the air.

Breeding. Mid-Feb to end of May. Tiny cup-shaped nest of brown plant down and spider web is built in forked twigs of shrubs, low woody herbs and dead annuals, 0.5-3 m above the ground. Several nests often found in close vicinity to each other. Clutch size 2; incubation 15-16 days, by



female; chick is black with sparse pinkish dorsal down; fledging at 20-23 days; young occasionally return to the nest shortly after fledging. Breeding success around 30%.

Movements. Sedentary. During the rainy season less numerous in coastal habitats.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Tumbesian Region EBA. A common species throughout range, with densities of at least 8-12 pairs/km². Readily accepts man-made habitats such as gardens and cultivated areas.

Bibliography. Becker & López (1997), Berg (1994),

Best & Clarke (1991), Best & Kessler (1995), Best *et al.* (1997), Butler (1979), Cook (1996), Marchant (1960), Meyer de Schauensee (1982), Parker *et al.* (1982), Pople *et al.* (1997), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Taczanowski (1884), Taylor (1995), Williams & Tobias (1994), Zimmer (1953a).



317

318

319

320

321

ssp. jourdani

with greenish gorget
ssp. torridus

with greyish
gorget

322

323

ssp. andinus

ssp. rosae

ssp. flammula

ssp. simoni

324

325

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328

Genus *CHAETOCERCUS* G. R. Gray, 1855

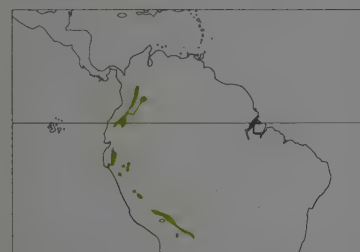
317. White-bellied Woodstar

Chaetocercus mulsant

French: Colibri de Mulsant **German:** Weißbauchelfe **Spanish:** Colibrí de Mulsant
Other common names: Mulsant's Woodstar

Taxonomy. *Ornismya Mulsant* Bourcier, 1842, Bogotá, Colombia. Usually placed in genus *Acestrura*, along with *C. bombus*, *C. heliodor*, *C. astreans* and *C. berlepschi*, but no evidence in external morphology justifies treatment in a genus separate from *C. jourdanii*. Two similar names for this species proposed by same author in quick succession, leading to some confusion: name *mulsant* was probably described very slightly earlier (perhaps roughly one month) than *mulsanti*. "*Calothorax decoratus*" is probably a hybrid of present species and *C. heliodor*. Monotypic.

Distribution. C & E Andes of Colombia patchily through Ecuador and Peru to C Bolivia (Yungas of Cochabamba).



Descriptive notes. c. 8.5 cm; c. 3-8 g. Male has straightish black bill; upperparts dark bluish-green, white postocular line behind eye joining broad white band on breast; gorget iridescent reddish-violet; rest of underparts like upperparts, vent white, white patch on flanks; tail forked, outer rectrices reduced to shafts. Eclipse male has pale white throat. Female bronzy-green above, greyish mask around eyes, postocular line buff; below tawny, throat pale cinnamon, belly and flank patch white; tail rounded, central rectrices green, outer cinnamon with broad black subterminal bar. Immature resembles female.

Habitat. Humid forest edges, highland pastures and cultivated areas, at 1500-2800 m, commonest above 2200 m, occasionally reported to 4000 m. Forages from near ground to canopy.

Food and Feeding. Little known; feeds on nectar of flowering *Agave*, *Inga* trees, *Lantana* and other small flowers; takes small arthropods. Subordinate to other hummingbirds, but by very slow humbee-like flight escapes attention of territory holders; does not establish feeding territories.

Breeding. One record of a nest at c. 10 m in a tree, Apr (Ecuador). No further information available.

Movements. Mainly sedentary; records at 4000 m suggest some seasonal dispersal.

Status and Conservation. Not globally threatened. CITES II. Uncommon to locally common, and seems to accept man-made habitats to some extent. Due to its small size the species is easily overlooked and is probably commoner than usually recorded. Has been recorded in Paschoa Forest Reserve (Ecuador).

Bibliography. Baez *et al.* (1997), Best *et al.* (1997), Bloch *et al.* (1991), Bond & Meyer de Schauensee (1943), Butler (1979), Chapman (1925a, 1926), Davies *et al.* (1994), Fjeldså & Krabbe (1990), Fritsch & Schuchmann (1988), Graves (1997b), Hilty & Brown (1986), Krüger *et al.* (1982), Parker *et al.* (1982), Prinzinger *et al.* (1981), Remsen & Traylor (1989), Schuchmann (1991), Schuchmann & Jakob (1981b), Schuchmann & Prinzinger (1987), Schuchmann *et al.* (1983), Snow & Snow (1980), Stotz *et al.* (1996), Taczanowski (1884), Williams & Tobias (1994), Wittmann (1982), Zimmer (1930, 1953a).

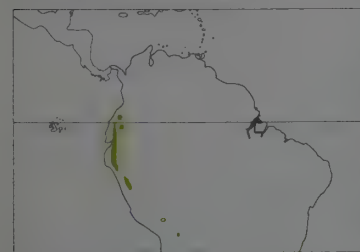
318. Little Woodstar

Chaetocercus bombus

French: Colibri bourdon **German:** Hummelfe **Spanish:** Colibrí Abejorro

Taxonomy. *Chaetocercus bombus* Gould, 1871, Citado, Ecuador. Usually placed in genus *Acestrura*, along with *C. mulsant*, *C. heliodor*, *C. astreans* and *C. berlepschi*, but no evidence in external morphology justifies treatment in a genus separate from *C. jourdanii*. Monotypic.

Distribution. Andes of extreme SW Colombia (S Nariño) and W Ecuador to N Peru; also locally in E Ecuador and NC Peru (Huánuco).



Descriptive notes. 6-7 cm. Male has straightish black bill; plumage generally dark bronzy blue-green, postocular line buffy white, curving around gorget to join buffy pectoral band; gorget rosy, rest of underparts bronzy blue-green; tail forked, outer rectrices reduced to shafts. Eclipse male has throat cinnamon-rufous, cheeks dark. Female bronzy-green above; below cinnamon, sides and vent tawny; tail rounded, tawny with black subterminal bar. Immature resembles adult female.

Habitat. Deciduous forest of transitional zone between humid and semi-humid region, from sea-level up to 2300 m in W Ecuador, at 900-

3000 m in E Ecuador and Peru. Forages from low to middle strata.

Food and Feeding. Records of food plants visited for nectar include flowering *Agave*, Asteraceae, *Cavendishia*, *Inga*, *Muntingia*, *Palicourea*, *Psamisia* and other Ericads. Foraging strategy presumably similar to *C. mulsant*.

Breeding. No information available; one record of displaying males in Mar.

Movements. Presumably sedentary, seasonal altitudinal dispersal most likely.

Status and Conservation. ENDANGERED. CITES II. Uncommon. The moist forest habitat of this hummingbird is under severe threat of deforestation, and in Ecuador, most has already been

destroyed. There are some forest patches remaining on steep slopes in the Ecuadorian and Peruvian Andes. Part of range in Ecuador is covered by Machalilla National Park, though protection there must be regarded as insufficient. Illegal logging and settling are the major threats, resulting in severe erosion, which damages remaining habitats. There have been few recent records of this species; however, only recently discovered to occur in Colombia, where recorded in Río Nambi Reserve, Jul 1996. Its importation into Europe is now regulated by national and international laws.

Bibliography. Baron (1897), Becker & López (1997), Best *et al.* (1997), Bond (1954), Butler (1979), Chapman (1926), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Fjeldså & Krabbe (1990), Kirwan & Marlow (1996), Knox & Walters (1994), Oberholser (1902), Parker *et al.* (1982), Paynter & Traylor (1977), Salaman & Mazariegos (1998b), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Taczanowski (1884), Wege & Long (1995), Williams & Tobias (1994), Zimmer (1930, 1953a).

319. Gorgeted Woodstar

Chaetocercus heliodor

French: Colibri héliodore **German:** Prachtkehlefe **Spanish:** Colibrí Heliodoro

Taxonomy. *Ornismya heliodor* Bourcier, 1840, Bogotá. Usually placed in genus *Acestrura*, along with *C. mulsant*, *C. bombus*, *C. astreans* and *C. berlepschi*, but no evidence in external morphology justifies treatment in a genus separate from *C. jourdanii*. Forms a superspecies with *C. astreans*. "*Calothorax decoratus*" is probably a hybrid of present species and *C. mulsant*. Two subspecies recognized.

Subspecies and Distribution.

C. h. heliodor (Bourcier, 1840) - Andes of Venezuela (Mérida), Colombia and W Ecuador.

C. h. cleavesi R. T. Moore, 1934 - Andes of NE Ecuador.



Descriptive notes. 5.8-6.4 cm. Male has straight black bill; plumage generally dark metallic blue-green; gorget pinkish-purple, elongated to form auricular tufts, breast grey, white spot on flanks; tail forked, central pairs of rectrices rudimentary, outer ones elongated and reduced to shafts. Eclipse male has pale throat, cheeks black. Female bronzy-green above, lower rump rufous; below cinnamon-rufous; tail rounded, cinnamon with black subterminal bar. Immature apparently resembles female. Male of race *cleavesi* differs in darker plumage, gorget less purplish, rectrices shorter and narrower.

Habitat. Edges of humid forest, coffee plantations and other disturbed areas with some trees and shrubs, at 1200-3000 m; occasional visitor to sub-*páramo*.

Food and Feeding. Feeds on nectar of flowering *Inga* trees, coffee and other tiny flowers. Insects are caught in the air by hawking. Forages from middle strata to canopy, strategy similar to that of *C. mulsant*.

Breeding. Nests in Apr-Oct (Mérida), fledglings in Oct (Ecuador). Nest cup-shaped, built of soft downy plant material like bromeliad seeds, externally decorated with lichens, pieces of dead leaves and small twigs, glued to vertical, or saddled on horizontal branch. No further information.

Movements. Some seasonal altitudinal movements likely.

Status and Conservation. Not globally threatened. CITES II. Relative abundance varies from rare to locally common. The paucity of records of this species may be in part due to its small size and inconspicuous behaviour. Range includes several national parks. In Ecuador, regularly recorded at Coca Falls and between Baeza and Tena. Report from Panama is erroneous, being based on misidentification of *Calliphlox mitchellii*.

Bibliography. Best *et al.* (1997), Butler (1979), Fjeldså & Krabbe (1990), Graves (1986, 1997b), Hilty & Brown (1986), Meyer de Schauensee (1964, 1982), Meyer de Schauensee & Phelps (1978), Moore (1934a), Olivares (1971), Olrog (1968), Robbins *et al.* (1985), Salaman & Mazariegos (1998b), Stotz *et al.* (1996), Wetmore (1968a), Wittmann (1982), Zimmer (1950c).

320. Santa Marta Woodstar

Chaetocercus astreans

French: Colibri des Santa Marta **German:** Santa-Marta-Elfe **Spanish:** Colibrí Astral
Other common names: Colombian Woodstar

Taxonomy. *Acestrura astreans* Bangs, 1899, San Sebastián, 6600 feet [c. 2000 m], Santa Marta Mountains, Colombia.

Usually placed in genus *Acestrura*, along with *C. mulsant*, *C. bombus*, *C. heliodor* and *C. berlepschi*, but no evidence in external morphology justifies treatment in a genus separate from *C. jourdanii*. Forms a superspecies with *C. heliodor*. Monotypic.

Distribution. Santa Marta Mts (NE Colombia).



Descriptive notes. c. 7 cm. Male has straight black bill; head shining green, rest of upperparts dark shining bluish; gorget reddish, elongated to form auricular tufts, breast grey, white spot on flanks; tail forked, central pairs of rectrices rudimentary, outer ones elongated and reduced to shafts. Eclipse plumage of male unknown; presumably similar to *C. heliodor*, with pale throat. Female bronzy-green above; below pale cinnamon-rufous; tail rounded, cinnamon with black subterminal bar, central rectrices green. Immature resembles adult female.

Habitat. Edges of montane forest, woodlands and shaded coffee plantations, occasionally in sub-*páramo*, at 825-2000 m.

On following pages: 321. Esmeraldas Woodstar (*Chaetocercus berlepschi*); 322. Rufous-shafted Woodstar (*Chaetocercus jourdanii*); 323. Volcano Hummingbird (*Selasphorus flammula*); 324. Scintillant Hummingbird (*Selasphorus scintilla*); 325. Glow-throated Hummingbird (*Selasphorus ardens*); 326. Broad-tailed Hummingbird (*Selasphorus platycercus*); 327. Rufous Hummingbird (*Selasphorus rufus*); 328. Allen's Hummingbird (*Selasphorus sasin*).

Food and Feeding. Takes nectar and insects; no specific food plants have been recorded, but presumably visits same flowers as congeners like flowering *Inga* trees and others; strategy similar to that of *C. mulsant*.

Breeding. No information available.

Movements. Seasonal altitudinal dispersal likely.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Santa Marta Mountains EBA. Locally common. No immediate threats have been recorded, though part of the habitat is under threat of deforestation; nevertheless, species readily takes to man-made habitats like coffee plantations. At present much of the range is inaccessible because of security restrictions.

Bibliography. Fjeldså & Krabbe (1990), Graves (1986), Hilty & Brown (1986), Salaman & Mazariagos (1998a), Stattersfield *et al.* (1998), Todd & Carriker (1922).

321. Esmeraldas Woodstar

Chaetocercus berlepschi

French: Colibri de Berlepsch German: Esmeraldaselfe Spanish: Colibrí de Esmeraldas

Taxonomy. *Chaetocercus Berlepschi* Simon, 1889, Ecuador.

Usually placed in genus *Aestrura*, along with *C. mulsant*, *C. bombus*, *C. heliodor* and *C. astreans*, but no evidence in external morphology justifies treatment in a genus separate from *C. jourdanii*. "*C. harteri*", known only from type specimen from Colombia, may be of hybrid origin. Monotypic.

Distribution. Pacific slope of Andes of W Ecuador (Esmeraldas, Manabí, Guayas).



Descriptive notes. c. 6-7 cm. Male has straight black bill; upperparts coppery green; gorget iridescent rosy violet, breast greyish-white; tail forked, outer rectrices reduced to shafts. Eclipse male has pale white throat. Female bronzy-green above; underparts white, throat tinged buff; tail rounded, tawny with black subterminal bar, tipped white, central rectrices green. Immature resembles adult female.

Habitat. Edges of lowland moist forest and second growth, from sea-level to 500 m, based on locality data on specimen labels.

Food and Feeding. Has been recorded as feeding on nectar of flowering *Inga* and *Muntingia*

calabura. Insects are caught in the air by hawking; forages mainly in canopy, using strategy similar to that of *C. mulsant*.

Breeding. No information available.

Movements. Unknown; altitudinal dispersal most likely.

Status and Conservation. ENDANGERED. CITES II. Restricted-range species: present in Tumbesian Region EBA. This hummingbird inhabits one of the most threatened forest habitats within the Neotropics. Large areas of moist forest have been destroyed during past years. Although the species may be recorded in second growth, it suffers severely from the loss of its natural habitat. Only some forest remnants are protected, though very poorly, within the Machalilla National Park.

Bibliography. Becker & López (1997), Best & Kessler (1995), Best *et al.* (1997), Butler (1979), Chapman (1926), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Dodson *et al.* (1985), Meyer de Schauensee (1982), Olrog (1968), Paynter & Traylor (1977), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Taylor (1995), Wege & Long (1995), Williams & Tobias (1994).

322. Rufous-shafted Woodstar

Chaetocercus jourdanii

French: Colibri de Jourdan German: Rotfahnenelfe Spanish: Colibrí de Jourdan
Other common names: Jourdan's Woodstar

Taxonomy. *Ornismya Jourdanii* Bourcier, 1839, Trinidad.

Often treated as sole member of present genus, but no evidence in external morphology for treatment in a different genus from those species traditionally placed in *Aestrura*. Three subspecies recognized.

Subspecies and Distribution.

C. j. jourdanii (Bourcier, 1839) - Trinidad and NE Venezuela (mountains of Cumaná).

C. j. rosae (Bourcier & Mulsant, 1846) - highlands of N Venezuela (Zulia to Distrito Federal).

C. j. andinus Phelps & Phelps, Jr., 1949 - Andes of Venezuela (Lara to Táchira) and E Andes of N Colombia.



Descriptive notes. 6-8 cm (including moderately long tail). Male has straight black bill; upperparts bottle green; throat violet, breast white, rest of underparts green, white patch on flanks behind wing; tail deeply forked, black with orange shafts. Eclipse male has throat cinnamon. Female is bronzy-green above; underparts rufous; tail two-lobed, cinnamon with dark subterminal bar, central rectrices green. Immature resembles adult female. Male of race *rosae* has throat rosy crimson; *andinus* is similar to previous, but throat more rose, less purple.

Habitat. Scrub, edge of montane forest, coffee plantations, occasionally sub-*páramo*, at 900-3000 m. Forages in middle to upper strata.

Food and Feeding. Has been recorded feeding on nectar of flowering *Inga* trees. Insects are caught in the air by hawking; employs same foraging strategy as *C. mulsant*.

Breeding. Birds in breeding condition and two immature individuals noted in Nov. Colombia. No further information available.

Movements. Seasonal altitudinal dispersal likely.

Status and Conservation. Not globally threatened. CITES II. Rare to locally common. Reported to be very rare in Trinidad. No immediate threats recorded, and species seems to take to man-made habitats like plantations. Occurs in Henri Pittier National Park (Venezuela).

Bibliography. French (1991), Fjeldså & Krabbe (1990), Herklotz (1961), Hilty & Brown (1986), Meyer de Schauensee (1982), Meyer de Schauensee & Phelps (1978), Olrog (1968), Phelps & Phelps (1949b), Stotz *et al.* (1996).

Genus SELASPHORUS Swainson, 1832

323. Volcano Hummingbird

Selasphorus flammula

French: Colibri flammule German: Vulkanelfe Spanish: Colibrí Volcanero

Other common names: Cerise-throated Woodstar/Hummingbird (*simoni*); Rose-throated Woodstar/Hummingbird (*flammula*); Heliotrope-throated Hummingbird (*torridus*)

Taxonomy. *Selasphorus flammula* Salvin, 1865, Volcán de Irazú, Costa Rica.

Nominate and race *torridus* have often been considered colour morphs of a single, variable taxon; alternatively, each has been treated as separate species; race *simoni* has been treated either as a separate species or as a race of *S. ardens*. Based on morphology, behaviour and breeding distributions, the three forms are best considered races of a single species; variation in gorget colour complicated and at present still imperfectly known, with some differences apparently being age-related. "*S. underwoodii*" is a hybrid between nominate race and *S. scintilla*. Three subspecies recognized.

Subspecies and Distribution.

S. j. simoni Carriker, 1910 - C Costa Rica (Volcanes Poás and Barba).

S. j. flammula Salvin, 1865 - C Costa Rica (Volcanes Irazú and Turrialba).

S. j. torridus Salvin, 1870 - S Costa Rica (Cordillera de Talamanca) and extreme W Panama.



Descriptive notes. 7.5-8 cm; male 2.5 g, female 2.8 g. Adult has short, straight, black bill; male of all forms has similar emargination on inner webs of rectrices 1 and 2, and unmodified remiges. Male bronzy-green above, central rectrices with some black towards tip, lateral rectrices mostly black edged and tipped with rufous; gorget mauve-purple, underparts mostly white, including collar across foreneck, sides of breast spotted with green and suffused with buffy to pale cinnamon. Female similar above, lateral rectrices with more or less rufous bases, black subterminal band, buffy to white tips; throat whitish, speckled with dusky

bronze. Immature resembles adult female but has extensive buffy fringes on the upperparts, more green and greyish and less rufous on the lateral rectrices and more (male) or less (female) emargination on the central rectrices. In race *simoni* both sexes average more buffy below and with more extensive black on tail, gorget of male rose red with lower margin squarer; both sexes of *torridus* similar but averaging whiter below, gorget of male metallic purplish-grey to purplish-green.

Habitat. Open brushy areas on high mountain slopes, including *páramo* and sub-*páramo*, bogs, scrubby second growth on landslide scars or volcanic ash deposits, scrubby highland pastures and roadsides, gaps and edges of stunted elfin forest and borders of taller forest. Breeds mainly from c. 2000 m to 3000-3500 m, locally as low as 1800 m.

Food and Feeding. Visits a wide variety of mostly small, often insect-pollinated flowers of shrubs (*Fuchsia*, *Rubus*, *Vaccinium*, *Castilleja*), vines (*Bomarea*), herbs (*Salvia*, *Digitalis*) and small trees (*Miconia*); takes advantage of perforations made by bumblebees or flowerpiercers (*Diglossa*) to reach nectar of flowers with long corollas, such as *Centropogon*. Male and sometimes female may defend feeding territories at large clumps of flowers, especially outside the breeding season, if not excluded by larger, more dominant species. Takes arthropods chiefly by flycatching; female in particular gleans from foliage, spiders' webs or roadcuts.

Breeding. Late wet and most of dry season, Aug or Sept-Feb. As early as Jul male defends as mating stations conspicuous lookout perches, usually near flowers, with chases and towering dive displays. Nest a compact little cup of pale-coloured plant down and spider web, heavily decorated on the outside with bits of moss and lichens, 1-5 m up on twig in outermost foliage of shrub or small tree, or on rootlet dangling under projecting bank of roadcut. No further information.

Movements. Following breeding leaves upper elevations, some descending to as low as about 1350 m and moving to adjacent mountains, producing some intermixing of races at this season.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species: present in Costa Rica and Panama Highlands EBA. Common over most of range, which includes protected areas for all forms such as Volcán Poás, Volcán Irazú and Amistad National Parks in Costa Rica. Rarest race is *simoni*, which also has most restricted breeding range, but even this form has probably benefited from deforestation and other human disturbances.

Bibliography. Anon. (1998a), Berlitz (1949a), Blake (1958), Carriker (1910), Farji (1991), Feinsinger (1980), Hainsworth & Wolf (1972b), Ridgely & Gwynne (1989), Ridgway (1911), Slud (1964), Stiles (1983a, 1985c), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968a), Wolf *et al.* (1976).

324. Scintillant Hummingbird

Selasphorus scintilla

French: Colibri scintillant German: Orangekehlfe Spanish: Colibrí Centelleante

Taxonomy. *Trochilus (Selasphorus) scintilla* Gould, 1851, Volcán de Chiriquí, 9000 feet [c. 2750 m], Panama.

Probably forms a superspecies with *S. ardens*. "*S. underwoodii*" is a hybrid between present species and *S. flammula*. Monotypic.

Distribution. Mountains from NC Costa Rica to W Panama, principally on Pacific slope.

Descriptive notes. 6.5-7 cm; male 2.1 g, female 2.3 g. Adult has short, straight, black bill. Male bronzy-green above, upperpart-coverts edged with rufous; tail broadly striped with black and rufous, the rectrices less emarginated than in *S. flammula*; outer remiges emarginated, produce a thin trilling sound in flight; gorget fiery orange-red, elongated at sides, set off by white collar across foreneck; breast and belly mostly cinnamon spangled with green, shading to whitish medially; vent and underpart-coverts rufous. Female has throat buff, speckled with grey; central rectrices largely green, lateral rectrices rufous with a broad black subterminal band. Immature resembles adult female but with rusty fringes on feathers of upperparts, especially on crown and nape; young male with much less green on central rectrices.

Habitat. Brushy forest edge, scrubby pastures, hedgerows, young second growth, coffee plantations and gardens; chiefly at altitudes of 900-2100 m (Costa Rica), 1400-2100 m (Panama).



Food and Feeding. Takes nectar from a variety of mostly small, often insect-pollinated flowers of shrubs and herbs (*Salvia*, *Hyptis*, *Lantana*, *Rubus*); at hedgerows of *Stachytarpheta* chiefly a furtive poacher in territories of larger, more dominant species. Takes arthropods mostly by hawking from perch, less often in bouts of prolonged hovering and darting; female in particular often gleans from low foliage or banks of roadcuts.

Breeding. Wet and early dry seasons, Sept-Feb (Costa Rica). During breeding season male occupies territorial posts in trees or tall shrubs overlooking open areas, often with *Salvia* flowers,

giving dive displays to repel or intimidate intruders. Nest a tiny cup of pale-coloured floss of thistles or other composites, grass heads, treefern scales and spider web, decorated with bits of moss and lichens, sometimes lined with small feathers, 1-4 m up on outside of large shrub or in grass tussock, often at edge of open space or on roadcut. No further information.

Movements. Outside breeding season may make limited altitudinal movements, sometimes moving upslope to c. 2500 m, or moving to other mountains to N and S of breeding areas.

Status and Conservation. Not globally threatened. CITES II. Restricted-range species; present in Costa Rica and Panama Highlands EBA. Scarce to locally common; has probably benefited from deforestation in many areas. In Costa Rica, has been recorded in several protected areas such as Volcán Irazú and Volcán Poás National Parks, and Monteverde Biological Reserve.

Bibliography. Anon. (1998a), Blake, E.R. (1956, 1958), Carriker (1910), Feinsinger (1977), Fogden (1993), Hartman (1957), Hernández-Baños *et al.* (1995), Ridgely & Gwynne (1989), Ridgway (1911), Slud (1964), Stattersfield *et al.* (1998), Stiles (1983a, 1985c), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968a).

325. Glow-throated Hummingbird

Selasphorus ardens

French: Colibri ardent

German: Feuerkehlfe

Spanish: Colibrí Ardiente

Taxonomy. *Selasphorus ardens* Salvin, 1870, Calovévora and Castillo, Panama.

Probably forms a superspecies with *S. scintilla*. Formerly considered closely related to *S. flammula simoni*. Monotypic.

Distribution. Mountains of WC Panama.



Descriptive notes. 7 cm. Adult has short, straight, black bill. Male bronzy-green above, rectrices black with rufous edgings and little emargination, outer primary attenuated; gorget pinkish-red, set off by white collar across foreneck; centre of breast and belly white, rest of underparts buffy to cinnamon, spangled with green, undertail-coverts buffy white. Female similar but throat pale buff speckled greyish, central rectrices largely green, lateral rectrices rufous basally, with black subterminal band and deep buffy tips. Immature resembles adult female but has rusty fringes on feathers of crown and nape and

more green on central two pairs of rectrices.

Habitat. Clearings and forest borders at elevations of 750-1800 m.

Food and Feeding. No information; presumably habits similar to those of *S. scintilla*.

Breeding. No information.

Movements. No information.

Status and Conservation. VULNERABLE. CITES II. Restricted-range species; present in Costa Rica and Panama Highlands EBA. Until recently, known from only two areas in the 20th century (Cerro Colorado/Cerro Flores, Santa Fé/Cerro Tute), where at best uncommon; neither area is protected. However, in Mar 1994 a hitherto unknown population was discovered in Cerro Hoya National Park, S Azuero Peninsula. Most of known (or suspected) distribution of species is inaccessible and apparently largely undisturbed; more information is required in order to evaluate its precise status and requirements.

Bibliography. Anon. (1998a), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Engelman (1994), Hernández-Baños *et al.* (1995), Renjifo *et al.* (1997), Ridgely & Gwynne (1989), Ridgway (1911), Stattersfield *et al.* (1998), Stiles (1983a), Stotz *et al.* (1996), Wege & Long (1995), Wetmore (1968a).

326. Broad-tailed Hummingbird

Selasphorus platycercus

French: Colibri à queue large

German: Breitschwanzelfe

Spanish: Colibrí Coliancho

Taxonomy. *Trochilus platycercus* Swainson, 1827, no locality = Mexico.

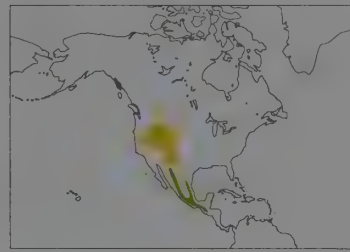
In past, occasionally placed in *Archilochus*. Proposed race *guatemalae* (Guatemala) is poorly defined; morphological patterns and variation in size are clinal in character. Monotypic.

Distribution. W & WC USA (S Idaho and N Wyoming) S to E California, Arizona and SW Texas) S through upland Mexico to highlands of Guatemala. N populations winter in Mexico and Guatemala.

Descriptive notes. 9.5-10 cm; 2.6-4.1 g. Male has short, straight, black bill; upperparts olive green; throat iridescent rose red, rest of underparts white with green flanks; central tail feathers bronze-green, rest dull purple-black with outer web edged cinnamon. Female golden green above; throat white, speckled greyish, breast and belly buff, more cinnamon on flanks and undertail-coverts; central tail feathers green, rest basally cinnamon, green in the centre, dark subterminal band, tipped white. Immature male similar to adult female but less distinctly cinnamon on outer rectrices; immature female similar to adult female.

Habitat. Sonoran belt of *Pinus*, *Juniperus* and *Cercocarpus* forests, riparian forests, arid pine-oak woodland, along streams with stands of *Salix*, subalpine meadows, at 1500-2500 m. Forages just above ground, usually 0.5-1 m.

Food and Feeding. Nectar of flowering shrubs and low-growing perennials, including *Penstemon*, *Ipomopsis*, *Castilleja*, *Salvia*, *Delphinium*, *Lonicera*, *Silene*, *Aquilegia*, *Robinia*, *Iris missouriensis*,



agaves, gooseberries and willow catkins. Insects are caught in the air by hawking or gleaned from coniferous foliage. Male establishes feeding territories at nectar-rich flower stands.

Breeding. In USA, Apr-Jun (Texas), May-Jul (Arizona), May-Jul (Colorado), Jun-Jul (Utah). Small cup-shaped nest of fine plant fibres, external wall decorated with lichen, pieces of bark and leaves, saddled on horizontal branch of willow, alder, pines, or fir at 1-4 m above ground, occasionally up to 9 m, often over water. Clutch size 2; incubation 16-17 days, by female; chick darkish with two rows of buffy

dorsal down; fledging period 18-26 days. First breeding in second year.

Movements. Sedentary in Mexico and Guatemala, migratory in USA. Male arrives in Arizona late Feb or early Mar, in Colorado late Apr to late May; migrates to Mexico early Sept. Altitudinal dispersal after reproduction.

Status and Conservation. Not globally threatened. CITES II. Locally common, especially in the Chiricahua Mts of Arizona, many parts of North American breeding range protected by national parks and nature reserves. Little information available on current state of habitat in Mexico and Guatemala.

Bibliography. Austin (1970b), Baicich & Harrison (1997), Bailey (1974), Baltosser (1989b), Banks & Calder (1989), Banks & Johnson (1961), Barash (1972), Bené (1947), Bent (1940), Binford (1989), Bourcicius (1993), Brody & Mitchell (1997), Brown & Kodric-Brown (1979), Bucher & Chappell (1992), Burleigh & Lowery (1942), Calder (1972, 1973a, 1973b, 1974b, 1975a, 1975b, 1981a, 1985a, 1991b, 1993b, 1995), Calder & Bonser (1973), Calder & Calder (1992), Calder & Hiebert (1982, 1983), Calder *et al.* (1983), Carpenter *et al.* (1983), DeGraaf & Rappole (1995), Des Granges (1979), Des Granges & Grant (1980), Dunford & Dunford (1972), Evanchik (1981), Friedmann *et al.* (1950), Grant & Grant (1968), Hainsworth & Wolf (1978), Hejl *et al.* (1995), Hering (1947), Howell & Webb (1995a), Huey (1944), Johnsgard (1979, 1997), Kaufman (1996), Kuban & Neill (1978, 1980), des Lauriers (1994), Lyon (1973), Manry (1995), Mayr & Short (1970), Medin & Clary (1991), Miller & Inouye (1983), Montgomerie & Redsell (1980), Nelson (1991), Ortiz (1971), Parrish (1988), Phillips (1975), Price *et al.* (1995), Pyle *et al.* (1997), Ridgway (1911), Schulz & Leininger (1991), Stiles (1971a), Stotz *et al.* (1996), Wagner (1946a, 1948, 1957b), Waser (1976, 1978, 1979), Waser & Inouye (1977), Wolf & Hainsworth (1986), Woodbury & Sugden (1938).

327. Rufous Hummingbird

Selasphorus rufus

French: Colibri roux

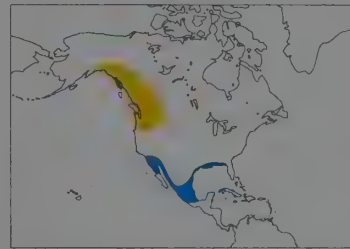
German: Rotrücken-Zimtelfe

Spanish: Colibrí Rufo

Taxonomy. *Trochilus rufus* J. F. Gmelin, 1788, Nootka Sound, Vancouver Island.

Forms a superspecies with *S. sasin*. Monotypic.

Distribution. Coastal SE Alaska S through SW Canada (British Columbia, W Alberta) to NW USA (Washington, N Idaho and extreme W Montana to N California). Winters throughout most of Mexico (except NC) and along Gulf coast of USA.



Descriptive notes. c. 8.5 cm; 2.9-3.9 g. Male has medium-short, straight black bill; crown bronze or bronze-green, remaining upperparts rufous, occasionally with a few green feathers on the back; throat iridescent scarlet-bronze to golden green, remaining underparts white on breast changing to rufous on lower belly; tail rounded, rufous above with black tips on central two pairs of rectrices, outer 3 pairs with black outer webs and dark greyish tips. Female is bronze-green on head and back; throat feathers often tipped with iridescent bronze, sometimes resulting in a large iridescent patch, rest of underparts including chin are dull white;

central rectrices metallic green, outer rectrices rufous, subterminally green and black, tipped white. Immature resembles adult female.

Habitat. Found typically in cool climates; in breeding range primarily in second growth forests; also frequent clearings and brushy areas where food flowers grow. Winter range is characterized by a wide variety of habitats, ranging from thorn forest and scrubland to mixed pine-oak-juniper forest. During migration frequents disturbed areas where food plants generally abundant.

Food and Feeding. Nectar from several plant species, and small arthropods. Flowers visited for nectar include *Agave*, *Aquilegia*, *Arbutus*, *Castilleja*, *Cleome*, *Epilobium*, *Linaria*, *Opuntia*, *Ribes*, *Rubus* and *Scrophularia*. Might also feed on sap from species such as alder (*Alnus*) and willow (*Salix*) through holes made by woodpeckers. Arthropods taken are primarily insects such as dipteran flies (*Anisopodidae*, *Chironomidae*) and Hemiptera (*Aleyrodidae*), and small spiders.

Breeding. Season likely timed with flowering of food plants. Nests are constructed in a wide variety of shrubs and trees; small nesting colonies have been reported. Nest is a cup lined with soft downy plant material, exterior covered with lichen, moss, or bark glued in place with spider web. Clutch size 2; incubation 15-17 days, by female; fledging at 20-21 days.

Movements. Migratory, wintering mainly in Mexico, in the central highlands; small numbers seen regularly in S Texas and along the Gulf coast of USA; rare in S California and also in Baja California, mainly in N. Southward migration, probably beginning Jun-Jul, follows two major flyways on either side of the Great Basin Desert, the western route following the Cascade and Coast Ranges and the Sierra Nevada, while the eastern route is along the Rocky Mts; arrives on wintering grounds Aug/Sept. Northward return migration takes place further to the west, along the Pacific coast; birds begin arriving in Washington late Feb and Mar. Timing of migration depends on flower availability.

Status and Conservation. Not globally threatened. CITES II. Some concern over a decrease in numbers during migration. In USA, artificial feeders maintain unusually large populations that exceed available natural food sources. The species is susceptible to natural or unnatural disturbances, such as forest fires, because its habitat is often restricted to the higher elevations of isolated mountain ranges. In the future, habitat destruction could prove to be a major concern throughout its range.

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328. Allen's Hummingbird

Selasphorus sasin

French: Colibri d'Allen **German:** Grünrücken-Zimtelfe **Spanish:** Colibrí de Allen
Other common names: Red-backed Hummingbird/Woodstar

Taxonomy. *Ornismya Sasin* Lesson, 1829, San Francisco.

Forms = superspecies with *S. rufus*. "*S. floresii*" usually reckoned to be hybrid of present species with *Calypte anna*. Two subspecies recognized.

Subspecies and Distribution.

S. s. sasin (Lesson, 1829) - coastal W USA (extreme S Oregon to California, S to Santa Barbara County); winters in SC Mexico.

S. s. sedentarius Grinnell, 1929 - islands off coast of S California (USA).

Descriptive notes. 8-9.5 cm; 2.5-3.8 g. Male has medium-short, slightly decurved black bill; plumage similar to *S. rufus*, with iridescent green on crown and back; gorget bright orange-red, breast white, with rufous on belly, sides and undertail-coverts; thigh feathers white. Distinguishable from *S. rufus* primarily by all-green back and crown which are more rufous on *S. rufus*. Female is metallic greenish-brown on crown and back; white below with scattered rufous spots, sides and undertail-coverts rufous; central rectrices are metallic green, outer rectrices rufous, subterminally green and black, tipped white. Immature similar to adult female. Both adult female and immature are difficult to distinguish from female *S. rufus*. Race *sedentarius* slightly larger and heavier than nominate, male has black tips on tail reduced, female has greener rectrices than nominate, white tips on outer rectrices larger.



Habitat. Scrubland, coastal chaparral, bushy slopes, open woodland and edges of redwood forest. During the breeding season *sasin* remains in riparian zones or humid canyons and ravines along the coast, but later in the summer begins a slow southward migration and is then found along the slopes of the Sierra Nevada in deciduous and coniferous vegetation. *Sedentarius* remains in scrubby canyons and ravines throughout the year.

Food and Feeding. Feeds on nectar of native shrubs and trees like *Nicotinia*, *Ceanothus*, *Arbutus menziesii*, *Agave*, *Mimulus langesdorffii*, *M. cardinalis*, *Stachys albens*, *Castilleja*

grinnelli, *Diplacus*, *Lonicera involucrata*, *Zauschneria californica* and introduced Myrtaceae, *Eucalyptus* and *Erythrina*. Insects are caught in the air by hawking.

Breeding. All year round (*sedentarius*), Feb-Jul (*sasin*). Nests are made of plant down, spider web, moss, lichens, hair, etc.; located outside male territories and placed inconspicuously on branch of conifer or deciduous tree. All nest building and care of young is performed by the female. Clutch size 2; incubation 15-22 days; fledging period 22-25 days; 1-2 clutches per season.

Movements. Migratory, race *sasin* wintering in C Mexico, with passage through NW Mexico drawn out over long periods; movement begins earlier than in other North American hummingbirds, males leaving breeding grounds between May and Aug, and most have left California by early Oct, as much as one month before females and juveniles. Return migration from Mexico can begin as early as Jan and territories can be established in N California from mid-Feb. Southward migration is through C Mexico and Arizona but the return movement is thought to be more concentrated in W Mexico. Individuals have been reported in numerous locations outside the traditional range, including in British Columbia, Massachusetts, Alabama and Kansas. Race *sedentarius* is sedentary. **Status and Conservation.** Not globally threatened. CITES II. Restricted-range species; present in California EBA. Breeding populations thrive near human settlements in, for instance, Santa Cruz and Berkeley (California). The species is common in canyons and scrub habitat along the coastal regions of California and S Oregon during the breeding season, and in similar Mexican scrub and forest habitat during the winter.

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